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THE STABILITY-DIVERSITY-COMPLEXITY DEBATE OF THEORETICAL COMMUNITY ECOLOGY: A PHILOSOPHICAL ANALYSIS

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THE STABILITY-DIVERSITY-COMPLEXITY DEBATE OF THEORETICAL COMMUNITY ECOLOGY: A PHILOSOPHICAL ANALYSIS

by

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DEDICATION

This dissertation is dedicated to my late Grandfather, Manford Logan. I wish I had had more time with him, and that he could see the work of his grandson.

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THE STABILITY-DIVERSITY-COMPLEXITY DEBATE OF THEORETICAL COMMUNITY ECOLOGY: A PHILOSOPHICAL ANALYSIS

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The stability-diversity-complexity debate has persisted as a central focus of theoretical ecology for half a century. The debate concerns the deceptively simple question of whether there is a causal relationship between the complexity and/or diversity of biological communities and their stability. Historical analysis of the debate shows that conflicting claims different studies seem to support indicate an underlying lack of conceptual clarity about the three concepts.

The problem of defining these concepts is thus at the debate's core, and finding adequate definitions is one objective of the dissertation. The absence of consensus about how ecological stability should be defined, for instance, reflects uncertainty about what properties of a community should

be considered its stability, resulting in studies that suggest conflicting conclusions based on different senses of the concept. For this reason, some philosophers have claimed that proposed definitions of ecological stability are incompatible and that the concept is itself problematic. I argue, however, that three unproblematic concepts are jointly sufficient and individually necessary for ecological stability. Another issue concerns whether the mathematical concept of Lyapunov stability utilized in physics adequately defines ecological stability, as many theoretical ecologists assume. I argue that it does not because it cannot adequately represent perturbations against which community stability must be assessed.

The project of defining these particular concepts raises a more fundamental issue: what adequacy criteria should definitions in general satisfy? Against the prevailing view that definitions must preserve meaning exactly, I argue there are good reasons to require definitions preserve only similarity of meaning with the defined concept. Following Carnap, I call such definitions 'explicative'. The prevailing view is clearly unproblematic if the definitional goal is simply to clarify the actual meaning of concepts. It is problematic, however, if the objective is to provide *normative* guidance about concepts. Concepts play an indispensable role in the acquisition of knowledge. As such, definitional modifications of our conceptual apparatus

should be evaluated by epistemic advantages or disadvantages they procure. I argue the advantages afforded by an explicative definition –such as enhancing precision, testability, theoretical unification, *etc*.– justify forgoing strong similarity with the concept being defined.

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CHAPTER 1: INTRODUCTION

The stability-diversity-complexity (SDC) debate has persisted as a central focus of theoretical ecology for half a century. The debate concerns the deceptively simple question of whether there is a relationship between the complexity and/or diversity of a biological community and its stability. From 1955, when Robert MacArthur initiated the debate, to the early 1970s, the prevailing view among ecologists was that diversity and complexity were important, if not the principal, causes of community stability. Robert May, a physicist turned mathematical ecologist, confounded this view with analyses of mathematical models of communities that seemed to confirm the opposite, that increased complexity jeopardizes stability. The praise May's work received for its mathematical rigor and the criticisms it received for its seeming biological irrelevance thrust the SDC debate into the ecological limelight, but subsequent analyses have failed to resolve it. Different analyses seem to support conflicting claims and indicate an underlying lack of conceptual clarity about ecological stability, diversity, and complexity.

At a coarse level of description, ecologists disagree little about the concepts of diversity and complexity. A biological community is a set of interacting populations of different species.[1] Its diversity is commonly understood

to be positively correlated with the number of species it contains (species richness), and how evenly individuals are distributed among these species (evenness) (Pielou 1975; Margurann 1988, 2004), though other possible components of diversity have been considered. Complexity of a community is positively correlated with its richness, how many of its species interact (connectance), and how strongly they interact. Diversity and complexity are similar properties and may be strongly positively correlated, but they are not identical. Species of a highly diverse community may interact little and therefore exhibit low complexity, and *vice versa*.

Beyond these relatively uncontested claims, disagreement arises over how the two concepts should be operationalized. Ecologists have proposed several mathematical functions that differ about what properties (species richness, evenness, connectance, *etc*.) are given priority over others in assessing diversity or complexity, and which differ in functional form. Currently, there is little agreement about what operationalizations, especially of diversity, are ultimately defensible (Ricotta 2005; Sarkar 2007).

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[1] Besides this weak condition about being composed of different species that interact, no stronger assumption is being made about what biological communities are or how they should be individuated. Ecologists typically make such determinations by convention: any biological system of scientific interest composed of at least two different species that interact in some way is taken to constitute a biological community. Chapter 4, Section 1 discusses the conventional nature of community specification in detail. Empirical issues about whether the biological world clusters into nonoverlapping sets of species that can be individuated by some nonconventional criterion, such as that there is much stronger causal interaction between species within a set than between those in different sets, are not addressed (see Sterelny 2001).

Another problematic aspect of the SDC debate is the lack of consensus about how ecological stability should be defined. This reflects uncertainty about what features of a community's dynamics should be considered its stability, and has resulted in conflicting conclusions about the debate based on studies using different senses of ecological stability (*e.g*. MacArthur 1955; May 1974; Tilman 1999; Pfisterer and Schmidt 2002). Ecological stability is not, however, unique in this regard. As McIntosh (1985, 80) has quipped: "A traditional problem of ecology has been that ecologists, like Humpty Dumpty, often used a word to mean just what they chose it to mean with little regard for what others said it meant." Disagreements about how to define concepts arise in other sciences as well. Careful analysis of the concept of ecological stability (and diversity and complexity) would thus help resolve the SDC debate, as well as illuminate the general problem of finding adequate definitions for concepts in science.

Besides providing insights about how problematic scientific concepts should be defined, the SDC debate also has a potential bearing on biodiversity conservation. For most senses of stability, more stable communities are better able to withstand environmental disturbances, thereby decreasing the risk of species extinction. Positive feedback between diversity/complexity and stability would therefore support conservation efforts to preserve biodiversity, assuming biodiversity and ecological diversity/complexity are closely related (see Goodman 1975; Norton 1987, Ch. 3 and 4; Izsák and Papp 2000; Sarkar 2007).

Finding adequate definitions for the concepts of ecological stability, diversity, and complexity, and defending a general account of definition due to Carnap that clarifies the desiderata these definitions should satisfy, are the two main objectives of this dissertation. To understand first what the SDC debate is about, the philosophical issues it raises, and the conceptual and methodological difficulties it faces, the second chapter, "Emergence of the Stability-Complexity-Diversity Debate: 1955-1975," introduces the SDC debate by critically tracing the history from its inception with MacArthur's (1955) influential analysis to May's (1974) upending of the near ecological consensus at the time that "diversity begets stability." The idea that there is a "balance of nature" was a staple of the schools of natural philosophy from which biology emerged long before the term 'ecology' was even coined (Egerton 1973). Some early ecologists such as Fredrick Clements and A. J. Nicholson continued this tradition by attempting to derive the existence of a "natural balance" in biological populations from organismic metaphors and analogies with physical systems (Clements 1916; Nicholson 1933; Kingsland 1995; Cuddington 2001). Not until Robert MacArthur's (1955) work, however, was the concept of a balance of nature precisely defined as ecological stability, and the predominantly metaphysical speculations about its cause superseded with a scientific hypothesis about its basis.

Besides considering MacArthur (1955) and Elton's (1958) arguments for a positive relationship between ecological stability and diversity/complexity, and showing why they fail, Chapter 2 also describes the mathematical character the debate acquired in the late 1960s and 1970s. Lewontin's (1969) analysis of the relationship between different mathematical concepts of stability and ecological stability, and May's (1974) study of stability and complexity in mathematical models of biological communities are especially important in this regard because they had a substantial impact on how the SDC subsequently evolved.

The problem of defining scientific concepts – ecological stability, diversity, and complexity – is at the core of the SDC debate. Part of this problem concerns how these *specific* concepts should be defined, which Chapters 4 and 5 take up for ecological stability, and diversity and complexity, respectively. Undertaking this task raises a more fundamental issue, however: what makes for a good definition in science and philosophy and why? The third chapter, "Explicative Definition: A Defense," attempts to answer this question.

Chapter 3 first sets the philosophical context by reviewing Carnap's (1950) account of explication, his technical term for one form of definition,[2] and Strawson's (1963) criticisms of it. Different definitions of ecological stability proposed in the literature illustrate Carnap's adequacy criteria for explication, and different ways they can be satisfied. *Contra* Strawson, these and other scientific

[2] See Carnap (1950, 7) and Chapter 3, Section 2.

definitions often sacrifice intuitive accord with the imprecise notion being defined to attain (i) formal rigor and integration with well-developed mathematical theories; and/or, (ii) easy, or at least feasible, empirical measurement. This differs from definitions found in philosophical contexts, which usually attempt to maximize intuitive similarity with the imprecise notion being defined (DePaul and Ramsey 1998).

The reason scientific definitions often accord intuitions less significance is that these definitions should help in determining the structure of the world, which is not reliably achieved by inspecting intuitions.[3] Given this objective, definitions should be judged according to how they contribute to scientific practice, which is the principal motivation underlying Carnap's conception of explication. Strawson and many other philosophers, however, regard definitions as the end products of conceptual analysis in which intuitions should provide the primary guidance, and therefore play the main role in constructing definitions. This view of definition, or at least the idea that intuitions should play some nontrivial role in the formulation of definitions, is unproblematic if the definitional goal is simply to clarify the meanings of ordinary concepts of natural language. Besides intuitions, linguistic studies of how words are used (Jackson 1998), and studies of the mental representation of concepts in the cognitive sciences (Goldman and Pust 1998) also

[3] The idea that some concepts better describe or are better aligned with the structure of "the world" than others should not be taken to presuppose some type of scientific realism. 'Better aligned' could be evaluated in terms of empirical adequacy or the generation of new technologies, for instance, by antirealists.

help achieve this goal, and results of such studies could (and perhaps should) inform the defining process on this view of definition. If the goal is to provide a better conceptual framework for determining what the world is like, however, Chapter 3 argues this conception of definition is indefensible.

The fourth chapter, "How Should Ecological Stability Be Defined?" has two parts. Numerous definitions of ecological stability have been proposed (Orians 1975; Pimm 1984; Grimm and Wissel 1997), so the first part systematizes distinct senses of the concept into a comprehensive taxonomy. This classification indicates what senses are compatible and reveals other relationships between them. The first part of this chapter also argues that the concepts of resistance, resilience, and tolerance jointly provide an adequate definition of the concept of ecological stability, and rebuts Shrader-Frechette and McCoy's (1993) criticism that it is "conceptually confused" or "inconsistent."

With the conceptual clarification this taxonomy provides, the second part of Chapter 4 argues that the common definition of ecological stability as Lyapunov stability is flawed. This definition pervades mathematical modeling in ecology because it integrates the imprecise concept of ecological stability into a well-developed mathematical theory that has been fruitfully utilized in other sciences. The theory of Lyapunov stability, however, fails to represent the domain of application of ecological stability adequately. This failure illustrates an

important limitation of the mathematical theory of Lyapunov stability within ecology.

The fifth chapter, "Concept Determination within Ecology: Ecological Complexity and Diversity," serves the same function for the concepts of ecological diversity and complexity as Chapter 4 did for ecological stability. It first reviews and evaluates existing adequacy criteria for diversity indices – such as that a diversity index should be maximal when individual organisms are equally distributed among species of a community and the more technical concavity condition. Two additional criteria are then defended. Based on this analysis, common quantitative indices of diversity found in the ecological literature are assessed against these criteria to determine which indices have a reasonable biological interpretation, identify properties of biological communities that should be part of a diversity index, and clarify the relationship between statistical indices developed in nonbiological contexts, such as information theory (Khinchin 1957), and the concept of ecological diversity. Only those indices that satisfy defensible adequacy criteria potentially bear on the SDC debate.

Most ecological work has focused on indices of diversity rather than complexity. Formulating a complexity index for models of biological communities that represent the mechanisms driving community dynamics with linear differential equations is unproblematic. An additive or multiplicative function of species richness, connectance, and mean linear interaction strength are

adequate complexity indices for these models (see May 1974). For models representing communities with nonlinear differential equations, however, how mean interaction strength should be assessed is unclear because different species may interact in disparate ways. Chapter 5 concludes by describing difficulties involved in devising a complexity index for nonlinear models of biological communities.

Together, Chapters 4 and 5 provide a conceptual framework for the concluding chapter, "Conclusion: Evaluating Stability-Diversity-Complexity Relationships." The general objective of Chapter 6 is to explain and emphasize that only a small and rather unimportant portion of the SDC debate has been addressed by the empirical studies and mathematical modeling of biological communities conducted thus far. The preceding chapters make clear that there are many senses of ecological stability, diversity, and complexity and thus numerous stability-diversity-complexity relationships involved in the SDC debate. Complete resolution of the debate requires evaluation of all these relationships, only a limited subset of which has been analyzed hitherto.

To determine what relationships have and have not yet been analyzed, Chapter 6 identifies the specific sense of stability and diversity/complexity analyzed in previous well-known studies. This helps uncover gaps in existing knowledge about stability-diversity-complexity relationships, and helps specify goalposts by which the SDC debate can eventually be resolved. It also reveals the

limited scope of hypotheses adduced thus far to explain a positive correlation between stability and diversity/complexity, such as the insurance hypothesis (Yachi and Loreau 1999; Lhomme and Winkel 2002) or the weak interaction effect (McCann *et al*. 1998). Due to the controversy it has generated, Chapter 6 also examines the dispute about whether David Tilman's (1996, 1999; Lehman and Tilman 2000) widely adopted definition of ecological stability biases the stability-diversity debate in the positive (Doak *et al*. 1998; Tilman *et al*. 1998).

CHAPTER 2: EMERGENCE OF THE STABLITITY-DIVERSITY-COMPLEXITY DEBATE: 1955-1975

1. **Introduction**.

To understand what the stability-diversity-complexity (SDC) debate is about and the conceptual and methodological issues it raises, this chapter traces its history. Rather than attempt to provide a comprehensive history of work done on the debate during this period, the goal is to use some of the most important work to illustrate why the debate remains unresolved, and to set the context for a detailed analysis of the concepts it involves in later chapters. The historical focus is therefore selective, but hopefully illuminative.

Section 2 begins by analyzing seminal works by Robert MacArthur, Charles Elton, David Pimentel, and others that elevated the previously poorly formulated question of whether more complicated biological communities are more "balanced" to the status of a scientific debate. Part of what this analysis reveals are the formidable theoretical and empirical challenges involved in evaluating stability-diversity-complexity relationships. Section 3 examines some technical attempts to define the concepts of the debate more precisely in the 1960s and 1970s, the most important of which was Lewontin's (1969) analysis of the relationship between the concept of ecological stability and mathematical concepts of stability. These attempts to define ecological concepts more precisely were part of a general trend towards greater emphasis on theoretical development

and mathematical modeling in ecology in the late 1950s and 1960s (Lewontin 1969; Kingsland 1995, Ch. 8). This section concludes by considering a negative response to this trend: Hurlbert's (1971) incisive critique of the concept of ecological diversity and the theoretically sophisticated, but biologically ungrounded quantitative indices he believed were being proposed for it. Robert May's analysis of mathematical models of biological communities epitomized and in many ways represents the pinnacle of the approach Hurlbert criticized, but it unquestionably brought greater mathematical rigor and sophistication to the SDC debate. Section 4 concludes this chapter by discussing his influential work and how it upended (but should not have) the popular belief among ecologists that "diversity begets stability." The historical scope of this chapter from 1955 to 1975 therefore represents a time period in which the SDC debate began, a strong consensus emerged about it, and this consensus dissolved.

2. **Origins of the Debate**.

Robert MacArthur (1955) published the first precise definition of ecological stability while still a graduate student of Yale ecologist G. E. Hutchinson. The paper, which was MacArthur's first publication, was an attempt to understand how the food web structure of a community could make it stable, and a definition of community stability was required to make the question precise. MacArthur's motivation for doing this analysis, about which the 1955 paper

provides little indication, was likely the lack of a scientifically rigorous explanation of the widespread view that community diversity enhances stability at the time (Ives 2005).

In an effort to clarify the vague attributions of a "balance of nature" to biological systems with a precise definition of ecological stability, MacArthur (1955, 534) first noted that ecologists tended to call communities with relatively constant population sizes stable, and those with fluctuating populations unstable. Stability in this sense denotes *constancy*. He thought, however, that this confused stability with its effects, and offered another account:

> Suppose, for some reason, that one species has an abnormal abundance. Then we shall say the community is unstable if the other species change markedly in abundance as a result of the first. The less effect this abnormal abundance has on the other species, the more stable the community. (1955, 534)

This account identifies the underlying dynamic responsible for constancy, not constancy itself, as the proper defining property of stability. Stability in this sense depends on how communities respond to disturbance, in this case the one abnormal abundance. Smaller changes in other species abundances are indicative of a more stable community. Although MacArthur did not use the term, this type of stability is a form of *resistance* to disturbance because its attribution to a community is based on the degree one abnormal abundance changes other species abundances – specifically, the degree to which other abundances resist changing –

rather than on whether the community returns to equilibrium.[4] For a community at equilibrium, *i.e*. its populations remain constant if the community is undisturbed, high resistance will ensure relative constancy is retained even if the community is disturbed. Highly resistant communities will therefore usually exhibit approximately constant species abundances through time, which MacArthur believed led many to call them stable. For MacArthur, however, constancy is a consequence of resistance, not equivalent to it.

MacArthur recognized that two properties could account for high resistance: (i) interspecific species interactions, such as predation and competition; and, (ii) "intrinsic" properties of species, specifically their physiologies. Focusing on (i),[5] MacArthur (1955, 534) suggested a "qualitative condition" for stability: "The amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community." 'Measure' in this condition is used in the standard statistical sense to represent the type of relationship exhibited between positively correlated properties, in the same sense that IQ is claimed to measure intelligence for instance. Thus, the qualitative condition assumes rather than supports the claim of a positive

[4] Orians (1975) and Webster *et al*. (1975) were probably the first to give this stability concept a distinct label. Orians called it 'inertia' and Webster *et al*. called it 'resistance.'

[5] MacArthur (1955) did not discuss (ii). In fact, since MacArthur defined stability as resistance to an abnormal abundance of some particular species, intrinsic physiological properties of species are only important determinants of ecological stability to the extent they affect interactions between them, specifically, on how species abundances affect one another.

correlation between community stability (understood as resistance) and food web structure.

MacArthur justified this assumption with an intuitive argument that a large number of links in a community's food web should make it highly resistant. In a food web where species *S* is atypically abundant, other species abundances are affected less the more widely *S*'s "excess energy" is distributed among different predators. Similarly, a wide variety of alternative prey for *S*'s predators would minimize the effects an abnormally low abundance of *S* would have on them. In either case, the number of links in a food web is positively correlated with community resistance. If correct, note that this argument *only* establishes a positive correlation. It does not justify conflating properties MacArthur used to define ecological stability (response to an abnormal abundance) with those that may be positively correlated with them (food web structure). Margalef (1958, 61), for instance, misinterpreted MacArthur's analysis in this way: "In [MacArthur's (1955)] sense, stability *means*, basically, complexity," (emphasis added).[6]

After noting that resistance can be quantified in several ways, MacArthur (1955, 534) proposed two "intuitive" adequacy conditions for doing so:

(i) resistance should be minimal (*e.g.* 0) for food webs with exactly one species at each trophic level (food chains); and,

[6] Ives (2005, 160) seems to adopt the same interpretation: "MacArthur (1955) who assumed that greater stability is *synonymous* with the number of pathways along with energy can flow through a food web and the equitability of energy flow among pathways," (emphasis added).

(ii) resistance should increase with the number of food web links.

Conditions (i) and (ii) refer to properties of food webs, not, as MacArthur *defined* resistance, to how communities change after one species becomes abnormally abundant. What do (i) and (ii) have to do with quantifying how communities change after one species becomes abnormally abundant? What MacArthur was in fact doing was proposing adequacy conditions for quantifying the *measure* of resistance he had just argued for: "the amount of choice which the energy has in following the paths up through the food web." Conditions (i) and (ii) were not intended to help quantify the concept of resistance as MacArthur *defined* it. Thus, adequacy conditions (i) and (ii) presuppose, rather than establish the truth of his intuitive argument about the relationship between food web links and resistance.

This explains how MacArthur could quantify resistance with the Shannon index:

$$(1) \qquad -\sum_i p_i \ln p_i;$$

where p_i is the proportion of the community's "food energy" passing through path i in the food web, which does not represent anything about how species abundances in a community are affected by the abnormal abundance of one species.[7] The decision to use this index, which he called "arbitrary," was intended

[7] MacArthur (1955, 534) defined a path as a series of links in a food web from producers to top consumers. Notice that MacArthur's use of Shannon's index differs considerably from the interpretation that became standard later in which p_i represents the proportion of individuals of species i in the community, and the index is intended to represent the diversity of a community

to specify a mathematical function satisfying (i) and (ii), although MacArthur (1955, 534) noted that it "may be significant" that (1) has the same form as standard measures of entropy and information (*cf.* Shannon 1948; Shannon and Weaver 1949).[8]

With this quantification of resistance, MacArthur described what properties of food webs would maximize it. For m-species communities, (1) is maximized when the species are at m different trophic levels and each level-k species ($k \leq m$) consumes all species at all lower levels. It is minimized when one species consumes the remaining $m-1$ species, which are all at a single, lower trophic level.[9] If the species consumed per consumer is held constant, moreover, (1) increases with species richness. This fact and the fact that (1) increases with the number of food web links entail either that large numbers of species with restricted diets, or small numbers that consume many different species can produce a particular value of (1). On this basis, MacArthur hypothesized that since species poor communities only have high values of (1) when consumers eat a wide variety of species, but consumer diets in species rich communities need not be similarly restricted to attain the same (1) value, species rich communities will usually be more resistant. This prediction may explain, MacArthur (1955, 535)

(see Ch. 5, §4). Good (1953) and Margalef (1958) were the first to use the Shannon index to represent diversity in this way.

[8] See Chapter 5, Section 4.

[9] In correspondence with Eric Pianka towards the end of his life, MacArthur alluded to doubts concerning this claim about minimization (Eric Pianka, personal communication). MacArthur unfortunately died before revealing the reason(s) for these doubts.

suggested, why Arctic communities, which usually contain fewer species than temperate and tropical ones, seemed to exhibit greater population fluctuations.

Compared with other ecological research of the time, MacArthur's analysis was one of the most mathematically sophisticated. Instead of focusing on empirical evidence, his primary concern was to formulate intuitive ideas about food web structure with mathematical precision and explore their implications. Unlike his predominantly data-driven contemporaries, Hutchinson encouraged this approach to ecological questions among his students (Kingsland 1995). Hutchinson believed speculative but mathematically rigorous analyses were crucial to stimulating novel approaches to recalcitrant problems (Hagen 1992). By challenging ecologists to pinpoint their shortcomings, which mathematical clarity helped facilitate, even those later found wanting would stimulate development of improved successors. Hutchinson used this argument, for instance, to defend publication of Lindeman's (1942) now classic paper on energy flow in ecosystems against referees of *Ecology*, who criticized it for being too theoretical and thus inappropriate for the journal (Cook 1977).

Sometimes, however, this kind of speculative research is uncritically accepted and treated as definitive. This was especially true of such work in post-WWII ecology. At that time, many ecologists thought their discipline suffered from a general lack of mathematical precision and the absence of a theoretical basis (Slobodkin 1953; Margalef 1958). For this reason, another Hutchinson

student, Lawrence Slobodkin, originally encouraged MacArthur to pursue graduate work in biology with Hutchinson after MacArthur had finished his master's degree in mathematics in 1953 (Kingsland 1995). Five years later Slobodkin (1958), praised MacArthur's (1955) analysis because he believed (erroneously) that it provided a general method for ranking the stability of different communities based on their qualitative food web structure,[10] and that this would in turn improve ecological theory by helping classify and conceptualize specific mathematical models. Slobodkin thought development of a "unified theory of ecology" required analyses like MacArthur's, and that they would remedy a troubling "trend in theoretical ecology towards each investigator developing his own equations and systems as if he were alone in the field" (1958, 551). But Slobodkin (1958) also accepted MacArthur's explanation of a positive relationship between ecological stability and food web structure without scrutiny. Hutchinson (1959, 149) similarly exaggerated and mischaracterized MacArthur's explanation as a "formal proof" based on information theory, and Pielou (1966, 163-164) cited only MacArthur (1955) to support the "fact" that stable communities are more diverse than unstable ones. These strong claims were especially unsubstantiated given that MacArthur's (1955) analysis was concerned

[10] The belief is erroneous because the value of the Shannon index depends on the quantitative value of the p_i (see [1] above).

only with communities exhibiting strictly predator-prey interspecific relations, not competitive, mutualistic, commensualistic, *etc*. relations.

Unfamiliar with MacArthur's work and more wary of ecological theory that was not closely tethered to data, British ecologist Charles Elton (1958) took a more empirical approach to the issue. Elton founded the famous Oxford Bureau of Animal Population in 1932 and was its director for more than three decades. Compared with the work of Hutchinson and his students, the research of the Bureau was concerned with more empirical and practical ecological projects, such as exhaustive biological surveys of small British islands and forests outside Oxford, and improving pest control methods for rodents during WWII (Crowcroft 1991). Out of this focus came a cautious skepticism of the biological relevance of Lotka and Volterra's mathematical models of biological communities, and similar approaches to ecological theory (Leibold and Wootton 2001). Specifically, for Elton (1958, 131), "there does not seem much doubt that theories that use the food-chain for an explanation of the regulation of numbers are oversimplified." Elton focused instead on empirical evidence that seemed to show that some communities were more resistant to invasion by exotic species than others, and experienced more population fluctuations than others. Several documented cases of biological invasions and pest outbreaks on islands and in ecosystems "simplified by man" – such as the giant snail (*Achatina fulica*) in Hawaii, the red deer (*Cervus elaphus*) in New Zealand, and the European red mite

(*Metatetranychus ulmi*) in orchards worldwide – were the main support for his analysis (see below).

Elton's concept of ecological stability had two components: resistance to invasion and constancy of populations (1958, 145). This differed from MacArthur (1955) in two ways. First, constancy was explicitly part of stability whereas MacArthur thought constancy was a byproduct of stability, and not an appropriate part of its definition. Second, Elton and MacArthur's concepts of resistance depend upon different types of disturbance. MacArthur's refers to a community's reaction to an abnormal abundance of one species. Elton did not explicitly define his concept of resistance, but it presumably refers to the ability to suppress the establishment, reproduction, and spatial spread of invasive species, *i.e*. to resist invasion. Ecological stability therefore involves resistance to disturbance for both Elton and MacArthur, but each focuses on different types of disturbance. Consequently, although Elton (1958) and MacArthur (1955) are commonly cited as analyzing the same relationship between stability and diversity (Pimm 1984; Lehman and Tilman 2000; McCann 2000), their analyses presuppose different stability concepts.

Their analyses also study different properties of a community's structure. Elton (1958, 145) did not explicitly define 'rich' and 'simple' in his claim that "simple communities...[rather than] richer ones...[are] more subject to destructive oscillations in populations, especially of animals, and more vulnerable to

invasions," but species richness, not food web structure as in MacArthur's analysis, was the primary focus of the six kinds of evidence he presented in its support (1958, 146-150):

(i) despite his skepticism about their ecological relevance, Elton noted that simple mathematical models of one-predator, one-prey communities predicted fluctuations of population sizes and often mutual extinction, even in the absence of external disturbances;

(ii) experiments on microscopic one-predator, one-prey communities exhibited the same behavior as these mathematical models. Elton (1958) cited Gause (1934), who showed that population fluctuations to the point of extinction were typical in simple protozoan communities;[11]

(iii) small oceanic islands with few species seemed to be more vulnerable to invasion than similar continental areas of the same size and, Elton assumed, more species;

(iv) successful invasions and population explosions of invasive species occurred more often in communities "simplified by man." Elton suggested four types of simplification as potential causes: (a) cultivation of exotic plants without introduction of the fauna normally accompanying them; (b) cultivation of these exotics in partial or complete monocultures; (c)

[11] Gause (1934) also showed that prey refuges could drastically influence the dynamics of these simple communities. Refuges did not end population fluctuations, but they usually did prevent extinction. On this basis, Elton (1958) presciently hypothesized that habitat structure and metapopulation dynamics may strongly influence the stability of natural communities.

eradication of species that reputedly harm cultivated plants; and, (d) selection of only a few genetic strains for cultivation;

(v) tropical communities, which contain more species and more complicated intra- and inter-specific dynamics than temperate communities, experienced fewer population explosions, especially of insects; and,

(vi) orchards, which are relatively simple ecological systems, were frequently successfully invaded. Elton suggested that pesticides usually decrease species richness in orchards and eradicate predators of herbivorous insects, which in turn facilitates invasions by exotic species and explosions in natural pest populations.

Since Elton included both constancy and invasion resistance in his concept of ecological stability, (i)–(vi) address different aspects of the SDC debate. (i) and (ii) focus on the lack of constancy, rather than invasibility, of microscopic communities and mathematical models of communities that contain few species. The lack of constancy, not invasibility, of temperate vs. tropical communities is also the focus of (v). On the other hand, (iii), (iv), and (vi) concern the greater invasibility of artificially simple or simplified communities – agricultural monocultures like orchards, for instance – and islands which contain relatively few species compared with continental regions of equivalent size.

Along with MacArthur (1955), Elton (1958) has frequently been cited in support of a positive stability-diversity relationship. Elton (1958, 146) was careful

to emphasize, however, the exploratory nature of his analysis, and he explicitly stressed the need for further data collection and study of the issue. An extensive review almost twenty years later (Goodman 1975), in fact, revealed some of the ways in which subsequent ecological work had failed to support Elton's predictions.

Goodman (1975) first pointed out that (i) and (ii) are only compelling if community models and microscopic communities with higher species richness exhibit less population fluctuation and fewer extinctions than those with fewer species, which was (and remains) unestablished.[12] Second, (iv) and (vi) were not based on controlled experiments and, Goodman further suggested, the simplified ecological systems in question may have achieved highly stable equilibria with their invasive pests were they not continually disturbed by cultivation. Third, (iii) is only compelling if the possibility that island communities are more susceptible to invasion than continental communities, irrespective of species richness, can be excluded as the cause of the pattern. Elton (1958) had not eliminated this possibility and Goodman noted that Preston's (1968) work on the evolution of island species might provide a better explanation of the greater invasibility of island communities than their supposed lower species richness. Fourth, the observations of population fluctuations in temperate regions and relative

[12] May's (1974) analysis of mathematical models of communities, for instance, seems to confirm the opposite (see §4).

constancy of tropical populations that constituted Elton's support for (v) had not been born out by subsequent studies. By the early 1970s, population fluctuations and insect outbreaks in the tropics that rivaled those in temperate regions had been observed (Leigh 1975; Wolda 1978). Their apparent preponderance in temperate compared to tropical regions was probably an artifact of the greater attention and resources devoted to the former.

While Elton's (1958) monograph was in press, Cornell entomologist David Pimentel (1961) conducted the first experimental test of a stability-diversity relationship in fallow fields outside Ithaca, New York. During the summers of 1957 and 1958, Pimentel planted wild cabbage (*Brassica oleracea*) in two fields, one containing approximately 300 plant species and another in which he removed all other plants. He then observed differences in the insect and arachnid communities that developed on individual *B. oleracea* plants in the two fields, and found that the densities of a few pest insects increased dramatically in the monoculture and that more herbivores resided on the monoculture plants than on those in the multi species community. Although Pimentel did not analyze the statistical significance of his results, he and other ecologists (*e.g.* Connell and Orians 1964) believed they showed that insect outbreaks were more severe in the

monoculture and thereby confirmed a positive relationship between ecological diversity and stability.[13]

One shortcoming of Pimentel's study is that diversity was narrowly measured as species richness in his experimental design and data analysis. Changes in species richness are relatively easy to measure, but they show nothing about changes in the proportions of individual organisms in each species of a community, *i.e*. changes in evenness, and little about community dynamics. Evenness is an important component of ecological diversity, so measuring diversity as species richness limits what Pimentel's study, and any other study using this diversity measure, can show about stability-diversity relationships.[14]

Even with this narrow measure, furthermore, it is unclear the experimental results justify Pimentel's (1961, 84) claim that, "The lack of diversity in...[the] single-species [monoculture] planting allowed outbreaks to occur." The problem is that there are two types of diversity in the monoculture field: plant and faunal diversity. In fact, the low plant diversity of the monoculture was accompanied by *increases* in insect and arachnid richness on the monoculture plants (higher than those on *Brassica* plants in the other field)[15] and the latter may have been a more

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[13] This claim continues to be made (*e.g*. Tilman 1999, 1457 and Ives 2005, 172) despite problems in Pimentel's experimental design and analysis discussed below.

[14] Pimentel (1961) should not be singled out for criticism. Almost all empirical studies of stability-diversity relationships use species richness as the surrogate for diversity, probably because evenness is so difficult to estimate in the field. Nonetheless, richness is a poor measure of diversity (see §3 below; Ch. 5; and Sarkar 2007).

[15] The differences were 27 taxa versus 50 in 1957, and 39 versus 50 in 1958 (Pimentel 1961, 79).

important determinant of outbreaks. Thus, while Pimentel interpreted his data as evidence of a positive relationship between diversity (measured as plant richness) and stability (absence of pest outbreaks), it could also be interpreted as evidence of a positive relationship between diversity (measured as insect/arachnid richness) and *in*stability (indicated by the outbreaks). Without separating the effects of plant species richness from insect/arachnid richness on outbreak likelihood, Pimentel's results do not provide unequivocal support of a positive stability-diversity relationship.

Another problem is that Pimentel created the monoculture by removing the extant plant community of one field, whereas *Brassica* individuals were comparatively unobtrusively added to the 300 species plant community of the other field. Removing extant plants undoubtedly initially eliminated predators of *Brassica* herbivores so that herbivores already on *Brassica* that were planted or that immigrated to the monoculture could reproduce unchecked, while herbivores in the other field faced their usual set of predators and did not increase. In other words, creation of the *Brassica* monoculture eliminated an important component of the extant animal community in that field, whereas the animal community of the other field was relatively undisturbed. The outbreaks may therefore have been a consequence of the disturbance that eliminated predators of *Brassica* herbivores, rather than the low plant species richness of the monoculture. Pimentel (1961, 84) recognized this potential confounding effect, and responded:

> the investigator doubts that the time-lag factor [*i.e*. that fauna had to immigrate to the plants in the monoculture] played a major role in the outbreaks, because wild *Cruciferae* were flourishing adjacent to all plots and provided ample sources of taxa for invasion of the single-species plots.

Whether this response is adequate or not, the problem could have been avoided if Pimentel had eliminated all the plants from both fields and then planted a monoculture and a multi-plant species community.[16]

In discussing his results, Pimentel's (1961) proposed two important hypotheses about possible causes of a positive relationship between species richness and constancy of populations. Pimentel may have been the first biologist to recognize that a "portfolio effect" might produce a positive relationship in the same way a diversity of investments usually reduces financial risk (1961, 84):

> Each host or prey species reacts differently to the same environmental conditions. One host population may decline as another host population increases. This tends to dampen the oscillations of the interacting host and parasite populations and provides greater stability to the system as a whole.

Although isolated one-predator, one-prey communities may fluctuate, this behavior is collectively averaged out in interactions between multiple predator and prey species so that these systems exhibit more constant total population sizes overall. Tilman (1996, 1999) has recently invoked this mechanism to explain an apparent positive correlation between ecological stability and diversity observed for Minnesota grasslands (see Ch. 6).

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[16] On the other hand, if the fauna had been preserved in the monoculture field – by transplanting insects and arachnids for instance – outbreaks may not have occurred.

Pimentel's (1961) second hypothesis assumes that the density of each prey species of a particular predator species is controlled by that predator within some density range. Perhaps below that range the predator may not detect the prey, and above it predation may not sufficiently suppress prey density. Given this assumption, Pimentel believed high numbers of different predator species would likely control prey densities for greater ranges. Thus, if an environmental disturbance favorable to a particular prey species caused its density to exceed a particular predator's control range, another predator species would likely suppress it in predator rich communities, especially if the communities contain predators that consume a wide variety of prey. Predator species diversity, therefore, functions to increase community resistance to environmental disturbance, and this in turn increases constancy of the community. This hypothesis has limited scope as a general account of putative stability-diversity relationships because it is restricted to purely predator-prey communities and depends crucially on the nature of the control mechanism exerted by predators on prey. However, the underlying idea, that stability increases as the number of species and their interconnections increase, was the focus of May's influential analysis of stability-complexity relationships (see §4 below).

3. **Mathematization of the Stability-Diversity-Complexity Debate**.

Although it was probably the first experimental study of the SDC debate, Pimentel's (1961) work received much less attention than the first theoretical analysis of the debate by MacArthur (1955). This likely reflected the transformation of ecology into a more mathematical and theoretical discipline occurring at the time. Largely through the work of Hutchinson and his students (most importantly MacArthur), mathematical modeling became more sophisticated and prevalent within ecology in the 1960s. Ecologists became increasingly concerned with formalization and theoretical systematization of ecological concepts (Kingsland 1995). Hutchinson's (1957) highly abstract set-theoretic definition of the niche as an *n*-dimensional hypervolume is one example, as were attempts to develop precise definitions and measures of ecological stability, diversity, and complexity by mathematically oriented ecologists around the same time. Lewontin (1969, 13) captured the intellectual shift within ecology: "To many ecologists their science has seemed to undergo a major transformation in the last 10 years, from a qualitative and descriptive science to a quantitative and theoretical one."

In the context of this transformation, the stability theory of linearized differential equations might have seemed to provide an adequate framework for evaluating stability-diversity-complexity relationships. For instance, the dynamics of a biological community near equilibrium could be represented mathematically with such equations, and formal stability criteria developed for them could be

used to assess whether the community was ecologically stable (see Ch. 4, §2). This was one of the methods utilized by Lotka and Volterra, for example, to analyze the stability of biological communities (*e.g.* Lotka 1925, Ch. 6; Volterra 1939).

A problem with this specific modeling strategy, however, revealed a general difficulty with the new theoretical orientation of ecology: achieving mathematical precision and rigor often made empirical measurement more difficult. For this reason, Patten (1961) criticized the ecological relevance of the stability theory of linear differential equations.[17] He pointed out that representing ecological systems with these equations involves numerous parameters that require extensive quantitative data to estimate accurately, data which are practically impossible to obtain in the field. To illustrate the problem, consider a community represented by:

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{A}\mathbf{x}(t); \tag{2}$$

where $\mathbf{x}(t)$ is a vector $< x_1, x_2, ..., x_i, ..., x_n >$ $(i = 1, ..., n)$ representing the densities of n species, and $\mathbf{A}$ is an $n \times n$ matrix of constant real coefficients $[a_{ij}]$ representing (linear) relationships between species near equilibrium, such as competition, predation, mutualism, *etc*. The problem Patten recognized is that the a_{ij} are

[17] Patten (1961) does not cite any specific ecologist as the target of his criticism, so the intended target may just have been a tacit assumption among ecologists that this was a useful method for analyzing the stability of biological communities.

extremely difficult to measure for complex, natural communities. Thus, "[s]ince it is usually not possible to obtain sufficient data to represent natural ecosystems canonically [as in (2)] and since they are probably not linear, formal stability criteria are not generally available for ecological applications" (Patten 1961, 1011).

Patten attempted to rectify this problem by proposing a more empirically tractable measure of community stability (*S*). It is based on time series data for variables x_i $(i = 1,...,n)$ representing species abundances or densities:

(3) $$S = \frac{1}{n}\sum_{i=1}^{n}\left|P_i\right|;$$

where *i* is an index of the *n* species; '|·|' denotes the determinant of '·'; and P_i are 2×2 matrices $\begin{bmatrix} p_{nd}^{i} & p_{nn}^{i} \\ p_{dd}^{i} & p_{dn}^{i} \end{bmatrix}$ in which p_{nd}^{i} is the probability of decrease in x_i following increase between two sequential time periods, p_{nn}^{i} is the probability of increase following increase, p_{dd}^{i} is the probability of decrease following decrease, and p_{dn}^{i} is the probability of increase following decrease. Since $\begin{vmatrix} p_{nd}^{i} & p_{nn}^{i} \\ p_{dd}^{i} & p_{dn}^{i} \end{vmatrix} = p_{nd}^{i}\,p_{dn}^{i} - p_{nn}^{i}\,p_{dd}^{i}$, the value of $\left|P_i\right|$ increases with the tendency of species *i* to *counteract* changes in its density. According to these definitions, if variable values do not remain constant for some time period, $p_{nd}^{i} + p_{nn}^{i} = 1$ and

$p^i_{dn} + p^i_{dd} = 1$.[18] Patten noted that $-1 \leq S \leq 1$, and suggested that $S < 0$ indicates instability and $S > 0$ indicates stability.

S can be applied to biological systems, such as ecological communities, as well as abiotic systems. Patten illustrated this by calculating *S* for a community of plankton species in the York River of Virginia, and for several abiotic variables representing the environment of the plankton: temperature, chlorinity, dissolved oxygen, *etc*. Measurements were made weekly for 10 weeks to estimate the transitional probabilities (p^i from above) of the plankton species and aquatic variables. Since these probabilities assume that variable behavior depends only on its immediately previous behavior, *S* treats these systems as Markov processes.[19] Patten found that the plankton species were 5.4 times more stable than abiotic variables representing their environment.

Conceptually, Patten suggested *S* measures "the resistance of the communities to change of state" (1961, 1010), which seems to accord with MacArthur's (1955) concept of ecological stability, and that it measures "the degree of homeostasis" (1961, 1011), which seems to connote a more general

[18] If the variables remain constant, p^i_{nd} and p^i_{nn} are not well-defined.

[19] Specifically, the p^i do not consider possible dependencies between values of variables that are nonsequential. Whether this Markov assumption accurately reflects the dynamics of biological communities is currently unclear. It seems to be incompatible, for instance, with the existence of delayed density dependence (see Stenseth 1999; Wootton 2001; Turchin 2003).

capability to remain unchanging.[20] In fact, *S* measures a property distinct from MacArthur's resistance, but essential to ecological stability.

Note that *S* is greatest when $p^i_{nd} = p^i_{dn} = 1$ and $p^i_{nn} = p^i_{dd} = 0$ for all *i*, *i.e.* when each species tends towards its original value after increase or decrease. In this case, the system will *likely* return to its original state following any disturbance that causes variables to change. The system will not *inevitably* return to its original state unless the magnitude of the subsequent increase (decrease) following decrease (increase) is always less than the initial change. If this is the case, the system will exhibit damped oscillations towards its original state. If this is not the case, the subsequent changes may increase in amplitude until species extinction occurs.[21]

The wide variety of different types and strengths of disturbances make it highly likely p^i_{nd} and p^i_{dn} will differ from unity and p^i_{nn} and p^i_{dd} will differ from zero. Some disturbances, for example, cause decreases in species density that precipitate extinction, which obviously precludes subsequent density increases of that species and makes $p^i_{dn} < 1$. The closer p^i_{nd} and p^i_{dn} are to unity and p^i_{nn} and p^i_{dd} are to zero, however, the higher the probability species *i* will return to its original value following disturbance. As these probabilities deviate from these

[20] Warburton (1955) had analyzed similar feedback mechanisms in the context of evolutionary theory.

[21] Patten did not consider this possibility, however, and his understanding of *S* as a measure of homeostasis assumes changes of increasing amplitude will not occur.

values, the likelihood of this return decreases. These probabilities therefore represent the likelihood a species (more generally, whatever the variables designate) will return to its initial value following a disturbance. As a function of these values, *S* consequently represents the likelihood a community (more generally, any system) will return to its initial state after disturbance. Since the likelihood a system returns to an initial state after being disturbed must be judged against different types and strengths of disturbances, systems with higher *S* values can sustain a wider variety and stronger disturbances and still return to the initial state. They will therefore return to their initial states more often after disturbance. Thus, *S* represents a kind of system *tolerance* to disturbance, which departed from earlier understandings of community stability as resistance or constancy.[22]

MacArthur also departed from his early understanding of stability as resistance in an analysis of predator-prey interactions. Working with one of his students, Michael Rosenzweig, MacArthur showed how different types of predator-prey relationships could be represented in graphs of their isoclines (Rosenzweig and MacArthur 1963). An isocline of a variable *x* is the set of its values for which $\frac{dx}{dt} = 0$. Different predator isocline shapes, they showed, represent different kinds of predator-prey systems. Depending on the isocline

[22] Orians (1975) was probably the first to give this stability concept a distinct label, 'amplitude.' It is commonly called 'domain of attraction' stability by ecologists (*e.g.* Grimm and Wissel 1997; Pianka 2000).

shape, the predator could be limited at an equilibrium density by its own density (*e.g*. by density-dependent competition), prey density, or both. Figure 1 illustrates an example of their technique.

On the assumption that predator-prey interactions near equilibrium are adequately represented by simple linear differential equations, Rosenzweig and MacArthur showed how well-known mathematical facts about stable equilibria could be graphically represented, and what the resulting representation indicated about predator-prey relationships. Unlike MacArthur's earlier work (MacArthur 1955), however, the concept of stability their analysis presupposed was based on the *rate* of return to equilibrium, not resistance. They demonstrated, for instance, that: "the prey slope must almost always be negative for stability and the greater the negativity of [the slope], the more stable the interaction" (1963, 220). Rosenzweig and MacArthur did not elaborate on the second clause of this statement, but the basis for it was that predator and prey densities return to equilibrium more rapidly the lower the value of the prey isocline slope. As a concept of ecological stability this later came to be known as *resilience*, and captures the idea that the quicker a community returns to a reference state after being disturbed, the more stable it is.[23] This concept of stability was distinct from MacArthur's earlier conception of stability as resistance. It is a stability concept

[23] Orians (1975), again, seems to have been the first to give this stability concept a distinct label, 'elasticity.' It is usually referred to as 'resilience' by ecologists today (*e.g*. Pimm 1984, 1991; Pianka 2000).

encountered frequently in applied mathematics, especially dynamic systems theory, however, and MacArthur's regular perusal of mathematical texts (Pianka and Horn 2005) may be responsible for his adopting it (see Ch. 4, §2).

With several distinct senses of stability in the ecological literature by the mid 1960s – resistance, resilience, tolerance, and constancy – it became clear to many ecologists that a critical assessment of the concept was needed.[24] The need for such an appraisal was not limited to ecological stability. Many fundamental but problematically unclear ecological concepts were being examined at that time to determine whether they could be reformulated within mathematical frameworks used in other sciences, especially physics (*e.g*. Kerner 1957, 1959; Lewontin 1969). Doing so would specify their meaning clearly and possibly integrate them into a common mathematical framework. Theoretical unification of this kind had proved fruitful in physics, and ecologists had similar aspirations for their discipline. The existence of a well-developed mathematical theory of stability made such a rethinking of ecological stability seem especially promising and in May a symposium at Brookhaven National Laboratory was ostensibly devoted to examining the meaning of stability and diversity (Woodwell and Smith 1969, v). Only one paper seriously addressed this task (Lewontin 1969), but it profoundly impacted the subsequent development of the SDC debate.

[24] See Chapter 4, Table 1 for a comprehensive list of different senses of stability found in the ecological literature.

Lewontin (1969) surveyed various mathematical notions of stability and their relation to ecological stability. He began by representing a biological community of n species as a vector $\mathbf{x}(t) =< x_1(t), x_2(t),..., x_n(t) >$ in an n-dimensional vector space H where t represents time. Different coordinates of $\mathbf{x}$ were intended to represent different abundances or densities of the n species in the community. A deterministic vector function $\mathbf{T}$ over H, $\mathbf{T}: H \to H$, represents the mechanisms responsible for the dynamics of the community.[25] $\mathbf{T}$ represents, therefore, density-dependencies, interspecific interactions, gene flow, *etc*. within and between the n species and the effects environmental parameters have on these species. $\mathbf{T}$ is often specified, for instance, in matrix form by a mathematical model of the community (*e.g.* [2] from above). Application of $\mathbf{T}$ to $\mathbf{x}$ usually induces a change in the vector's coordinates. Points in H for which $\mathbf{T} = \mathbf{I}$, where $\mathbf{I}$ is the identity matrix, induce no change in $\mathbf{x}$ and are called equilibrium points. A vector at such a point will not move from it.

Within this framework, Lewontin distinguished "neighborhood" stability (also called local Lyapunov stability) from global stability. Let $\mathbf{x}_q$ be the position vector for some equilibrium point. Following the mathematical theory of stability pioneered by Lyapunov (1892 [1992]), $\mathbf{x}_q$ is neighborhood stable if and only if for any $\mathbf{x}$ *arbitrarily close* to $\mathbf{x}_q$:

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[25] Note that $\mathbf{T}$ defines a vector field on H.

(4) $\lim_{n\to\infty} \mathbf{T}^n(\mathbf{x}) = \mathbf{x}_q;$

where $\mathbf{T}^n(\mathbf{x})$ designates *n* applications of **T** to **x**. The subset of *H* within which vectors satisfy (4) defines the *domain of attraction* of $\mathbf{x}_q$. Restricting attention to vectors arbitrarily close to $\mathbf{x}_q$ allows approximation of **T** by a linear vector function **L**. In effect, **T** behaves as a linear vector function arbitrarily close to $\mathbf{x}_q$. This linearization of **T**, in turn, allows evaluation of (4) with well-known mathematical techniques (see Hirsch and Smale 1974). If (4) holds for all of *H* and not just arbitrarily close to $\mathbf{x}_q$, $\mathbf{x}_q$ is called globally stable.

By representing the perturbation of a biological community as a displacement from $\mathbf{x}_q$ to **x**, the community's stability can be described by local and global stability. The set of perturbations (represented by the displaced vectors **x**) for which the community returns to equilibrium (represented by $\mathbf{x}_q$) determines its attraction domain. In ecological terms, locally and globally stable communities are often informally characterized as those that return to equilibrium after "very small" perturbations – such as slight climatic disturbances perhaps – and those that return after *any* perturbation.[26]

Lewontin (1969, 16) argued local stability inadequately defines ecological stability because it only describes system behavior arbitrarily close to a particular point in *H*. Strictly speaking, therefore, local stability only describes system

[26] See Chapter 4, Section 2 for a detailed criticism of defining ecological stability in this way.

behavior for *infinitesimal* displacements from $\mathbf{x}_q$. Real-world perturbations, however, are obviously not infinitesimal in magnitude. Any real perturbation will expel a system at a strictly locally stable equilibrium from its infinitesimal stability domain. In the same Brookhaven symposium, Preston (1969) also emphasized the fundamental obscurity of how infinitesimal displacement can be biologically interpreted (or empirically measured). Local stability therefore says nothing about system response to real-world perturbation. In contrast, Lewontin suggested that the stability of an ecological system depends upon the (non-infinitesimal) size of its attraction domain. If the formally precise notion of 'arbitrarily close' is informally construed as 'very close,' moreover, local stability still only describes system behavior for very small perturbations and thus provides little or no information about attraction domain size.[27] For this reason, local stability poorly defines ecological stability.

Local and global stability also poorly define ecological stability, Lewontin added, because they are dichotomous concepts, whereas biological communities seem to exhibit different degrees of stability. Elton and MacArthur's concepts of ecological stability confirm Lewontin's claim: Elton believed monocultures were *less* stable than "natural" communities, and the Shannon index MacArthur used to operationalize stability obviously takes values other than 1 and 0. The concepts of

[27] Of course, if **T** were linear over all of *H*, local and global stability coincide (May 1974). The dynamics of almost all ecological systems, however, are nonlinear.

tolerance and resilience underlying Patten's (1961) and Rosenzweig and MacArthur's (1963) conceptions of ecological stability are matters of degree also.

These distinct senses of stability also have natural counterparts in Lewontin's framework. Consider the domain of attraction D of some equilibrium $\mathbf{x}_q$. Tolerance – roughly, an ecological system's ability to withstand disturbance and still return to equilibrium – can be represented by the size and configuration of D. Whether an ecological system represented by $\mathbf{x}$ returns to $\mathbf{x}_q$ after being disturbed depends on the strength and type of disturbance. Regions of D far from $\mathbf{x}_q$ represent strong system tolerance to types of disturbance for which it can be severely disturbed and still return to $\mathbf{x}_q$. Regions of D close to $\mathbf{x}_q$ represent weak system tolerance to types of disturbance for which it can only be disturbed slightly and return to $\mathbf{x}_q$.[28] Resilience – roughly, the rate an ecological system returns to equilibrium after being disturbed – can be represented by the "steepness" of D.[29] A system in a steep domain of attraction like D will return to $\mathbf{x}_q$ rapidly after being disturbed from it. An unperturbed system at $\mathbf{x}_q$, furthermore, will remain stationary (constant) at $\mathbf{x}_q$.

Resistance, which Lewontin (1969) did not discuss, can also be conceptualized in this framework as the tendency of the system to remain near $\mathbf{x}_q$ following disturbance. MacArthur's (1955) concept of resistance, for instance, is

[28] Determining tolerance therefore requires a distance measure between vectors.

[29] "Steepness" of a domain of attraction is determined by the gradient (∇) of the vector function ($\mathbf{T}$) describing the system's dynamics, $\nabla\mathbf{T}$ (see Ch. 4, §2.3).

measured in terms of how other species abundances change in relation to the abundance of one species that has been disturbed to an atypical level. If this disturbance is represented by displacement of **x** in a particular direction of H,[30] resistance can be represented by how **x** behaves after displacement, specifically, by its subsequent deviance from $\mathbf{x}_q$ or lack thereof.[31] Each of these four concepts of ecological stability – resistance, resilience, tolerance, and constancy – has a counterpart within Lewontin's vector space framework.[32]

Lewontin drew an important distinction between stability as a perturbation-based concept, which resistance, resilience, and tolerance are, and nonperturbation-based concepts, such as constancy. Constancy, Lewontin (1969, 21) suggested, "is a property of the actual system of state variables. If the point representing the system is at a fixed position, the system is constant. Stability, on the other hand, is a property of the dynamical space in which the system is evolving." The two concepts are therefore different and not necessarily coextensive. A system in a large, steep domain of attraction, for instance, may be in constant flux due to frequent external perturbations. Conversely, an

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[30] Specifically, the abnormal abundance of one species would be represented by a change in one coordinate of **x**.

[31] Notice, however, that MacArthur's (1955) concept of resistance does not *require* the community return to a predisturbance state like an equilibrium.

[32] The stability concepts of resistance, resilience, and tolerance have *counterparts* in Lewontin's framework, but they are not adequately *definable* within it. The problem is that only disturbances of a particular kind – those that affect only system variables and leave system parameters unchanged – are representable in Lewontin's framework. Chapter 4, Section 2 argues resistance, resilience, and tolerance must be defined with respect to a broader, more realistic conception of disturbance that recognizes that disturbances can change system parameters.

unperturbed system may be constant at an unstable equilibrium. Partly for this reason, Chapter 4 argues ecological stability should not be defined in terms of constancy.

Lewontin briefly described one additional stability concept, structural stability. Andronov and Pontrjagin (1937) introduced this concept in an analysis of vector fields on the Euclidean plane, and Peixoto (1959) generalized the concept for *n*-dimensional systems. Informally, the property the concept represents is that small changes in the parameters of the equations describing a vector field do not change the topology of the vector field. Within biology, little or no work was devoted to this concept until the mathematician René Thom (1970, 1975) made it the basis of catastrophe theory. This theory categorized different ways systems may fail to be structurally stable, *i.e*. bifurcate, into distinct qualitative types. Thom then attempted to explain a wide variety of putative bifurcation processes in nature with this classification, for example, in geology, crystal formation, and biological morphogenesis.[33]

In an ecological context, if *R* is a set of equations that describe a vector field **T** representing the dynamics of a biological community, **T** is structurally stable if and only if, "a very small change in parameters [of *R*] will make a very small change in the configuration of the vector field [**T**]" (Lewontin 1969, 21).

[33] A better understanding of the structural stabilities and instabilities involved in the concept of a morphogenetic field within embryology, however, was Thom's (1975) main focus of application of catastrophe theory. The well-known embryologist C. H. Waddington, for instance, wrote the foreword to Thom's text.

Specifically, very small changes in parameters of *R* should produce little change in the number, position, or configuration of equilibrium points, limit cycles, and other attractors of **T**.[34] The resulting vector field should be, May (1974, 17) later clarified, topologically isomorphic to the original vector field.

Neither Lewontin nor May pursued the project of defining ecological stability as structural stability, and both focused on Lyapunov stability instead. Rather than reflect a judgment that structural stability is irrelevant to ecology,[35] their decision more likely reflects the fact that structural stability is a much more technically complex mathematical concept than Lyapunov stability, and that its application within ecology therefore appeared to be much more difficult.[36]

Compared to the concept of ecological stability, less attention was devoted to clarifying the concept of ecological diversity or complexity in the early SDC debate. Significant disagreement about how the concept of diversity should be measured, however, emerged during the 1960s (Magurran 1988, 2004).[37] By the early 1970s, moreover, enough attention was being devoted to common indices of

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[34] A limit cycle corresponds to a periodic solution of a set of differential equations towards which the system is asymptotically attracted. An attractor is any solution set towards which a system is asymptotically attracted (see Ch. 4).

[35] May (1974, 18) suggested that structural stability "is likely to be one of the growth points of theoretical ecology."

[36] Lewontin's (1969, 22) hope that, "structural instabilities will prove to be the exception," rather than the norm, in any case, had been invalidated by Smale's (1966) proof, cited by May (1974), that structurally stable systems are rare (more precisely, not dense) among systems with more than three variables.

[37] In contrast, the issue of how the complexity of a biological community should be measured received little or no attention within ecology during this period. Chapter 5 addresses this issue and analyzes the concept of ecological diversity in detail.

diversity to spark criticism, perhaps the most incisive from Hurlbert (1971) (see below).

Conceptually, ecologists at the time widely agreed that diversity has two main components: species richness and evenness (see Ch. 1 and 5). Distinct quantitative diversity indices result from different ways of quantifying and integrating these two notions. For a clearer understanding of these concepts, consider two simple communities, A and B, both composed of two species s_1 and s_2. A and B have the same species richness. If the percentages of individuals distributed among the two species are .02% and 99.98% for A and 50% and 50% for B, respectively, B seems more diverse than A. This can be represented by a higher evenness value for B. Besides that a diversity index should increase with species richness, therefore, another reasonable adequacy condition seems to be that it should increase with evenness. Many distinct quantitative indices, however, satisfy these two adequacy conditions (see Ch. 5, Table 2).

Probably the most popular index of community diversity, then and now, is the Shannon index (H) (see equation [1], §2). The index was originally intended to quantify the amount of information in a communicated message (Shannon and Weaver 1949). Good (1953) and Margalef (1958) were the first to use it as an index of diversity. In the ecological context, p_i designates the proportion of individuals in the i-th species of a community, so that H is at its maximal value

for a given species richness n (H = ln(n)) when the individuals are equally distributed among the species.

Another common diversity index (D) is the complement of Simpson's (1949) "measure of concentration":

(5) $$1-\sum_{i=1}^{n} p_i^2 .$$ [38]

Simpson (1949) explained that his concentration index represents the probability that two individuals chosen at random (with replacement) from a community will belong to the same species, so D represents the probability the two individuals will belong to different species. This probability, like Shannon's index, is at its maximal value for a given species richness n ($D = 1 - \frac{1}{n}$) when individuals are equally distributed among the species. D is more sensitive to the abundances of species and less sensitive to species richness than Shannon's index (May 1975; Magurran 1988, 2004).[39] Hurlbert (1971) later proposed, furthermore, that if D is multiplied by $\frac{N}{N-1}$, the resulting index represents the probability of interspecific encounter in the community.[40]

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[38] The inverse of Simpson's concentration index, $\frac{1}{\sum_{i=1}^{n} p_i^2}$, is also a common index of diversity (Levins 1968).

[39] Rényi (1961) showed that the Simpson and Shannon indices are members of a family of entropy measures (see Ch. 5).

By the late 1960s, a large number of diversity indices had been developed, and numerous empirical studies of different ecological systems were being conducted to estimate diversity using these indices (Pielou 1975; Magurran 1988, 2004; Sarkar 2007). In an influential critique of this ecological research agenda, Hurlbert (1971, 577) argued that, "the term 'species diversity' has been defined in such various and disparate ways that it now conveys no information other than 'something to do with community structure'," and that this indicated a fundamental vagueness of the underlying concept. He thought ecologists had further exacerbated this problem by appropriating statistical measures of diversity developed in nonbiological contexts with dubious ecological relevance. Rather than attempt to rehabilitate the concept by proposing adequacy conditions by which to evaluate the relative merits and weaknesses of different indices,[41] therefore, Hurlbert suggested the search for stability-diversity relationships should be refocused on the relationship between community stability and indices that reflect biologically meaningful properties that might influence community dynamics. His index of the probability of interspecific encounter is one example. Species richness seems to fail this test since it is generally unlikely that extremely rare species (*e.g.* s_1 in community A above) play an important role in community

[40] Sugihara (1982) later pointed out that this interpretation of *D* assumes that the frequencies of interspecific encounters are proportional to the relative abundances of the species (see Ch. 5, §3).
[41] Chapter 5 takes this project up in detail.

dynamics.[42] Species richness was and remains, however, the predominant measure of diversity in analyses of stability-diversity relationships (*e.g.* Tilman 1996, 1999).

4. **The End of the Consensus**.

By the early 1970s, a strong consensus had emerged that ecological diversity/complexity is positively correlated with, and probably causally responsible for, the stability of communities (May 1974, 37; Levins 1974, 129; DeAngelis 1975, 238; Pimm 1991, 9-10).[43] In a textbook on environmental science, for instance, Watt (1973) deemed the claim that biological diversity promotes population stability a core principle of the discipline. A half decade later, the consensus had evaporated. The main reason for its demise was the publication of rigorous analyses of mathematical models of communities that seemed to show increased complexity actually decreased stability.

In a one-page *Nature* paper, Gardner and Ashby (1970) initiated the first doubts with an analysis of the relationship between complexity and asymptotic

[42] This is not to deny there are cases in which very rare species play an important role in community dynamics.

[43] At that time, a clear distinction between diversity – which depends upon how individuals are distributed among the species of a community – and complexity – which depends upon how species interact in a community – had not been made within the context of the SDC debate. Recall from Chapter 1 that both diversity and complexity increase with species richness, but complexity may decrease with increasing evenness (and *vice versa*) and diversity may decrease with increasing connectance and species interaction strength (and *vice versa*). See Chapter 5.

Lyapunov stability in linear models such as (2) from above.[44] Understood as a model of a biological community, the coefficient a_{ij} from (2) represents the effect of species j on species i. Its quantitative value represents the effect's magnitude and its sign represents whether the effect is positive or negative. For these models, complexity was defined in terms of the number of variables (n) and connectance (C). Gardner and Ashby defined connectance as the percentage of nonzero coefficients in **A**.

Values of the diagonal elements of **A** were randomly chosen from the interval [–1, –0.1] to ensure each variable was "intrinsically stable," *i.e.* self damped. In models of biological communities, a diagonal element (a_{ii}) of **A** represents the intra-specific effect of species i on itself. Since its quantitative value represents the effect's magnitude and its sign represents whether the effect is positive or negative, negative values represent a self-damping effect, as could be caused by overcrowding as a population increases, for example. For given values of n and C, Gardner and Ashby then randomly distributed an equal number of –1 and +1 values within the off-diagonal parts of **A** in accord with the C value. Whether systems represented by (2) are stable depends upon the eigenvalues of **A**. These are scalar value roots λ_i of the characteristic polynomial of **A**, $|\mathbf{A}-\lambda\mathbf{I}|=0$,

[44] Gardner and Ashby (1970) analyzed linear models. Since nonlinear models can be linearized in the local neighborhood of an equilibrium if they are differentiable, the relationship Gardner and Ashby found between stability and complexity for linear models also holds between *local* stability and complexity of *linearized* models.

where **I** is the identity matrix. Lyapunov ([1892] 1992) proved an equilibrium of a system represented by (2) is asymptotically stable iff:

(6) $\mathrm{Re}\lambda_i(\mathbf{A})<0$ for $i=1,\ldots,n$;

where $\mathrm{Re}\lambda_i(\mathbf{A})$ designates the real part of λ_i, the i-th eigenvalue of **A**. Whether (6) holds depends on the pattern of nonzero values within **A**. Different randomizations specify different patterns, which may produce different stability results as evaluated by (6). The probability of stability for given values of n and C can therefore be approximated with results from a sufficiently large number of randomizations. Contrary to most expectations, Gardner and Ashby found the probability of local stability was negatively correlated with n, and with C. Interpreted ecologically, their analysis seemed to show that more species (greater n) and a higher the frequency of species interaction in a biological community (greater C) makes it less likely to be (locally) stable.

The study that inverted the opinion of most ecologists, however, was published by Robert May three years later (May 1974). One reason for its influence was that May generalized Gardner and Ashby's analysis by randomly assigning non-diagonal elements values from a distribution with a zero mean and mean square value of s^2 for different values of s. s represents the interaction strength between variables, which had been restricted to +1 and –1 by Gardner

and Ashby.[45] May then analyzed how the probability of (local Lyapunov) stability changed with different values of n, C, and s; Gardner and Ashby had not analyzed how s affects the probability of stability. The main result was that for systems in which $n>>1$, there is a sharp transition from high to low probability of stability as s or C exceeds some threshold. He found, for instance, that the probability of stability for these systems is approximately 1 if $s\sqrt{nC}<1$ and approximately 0 if $s\sqrt{nC}>1$. His analysis also confirmed Gardner and Ashby's finding that for fixed C and s the probability of local stability decreases with increasing n. In general, these results seemed to demonstrate that high connectance, species richness, or strong species interactions preclude communities from being stable. May defined complexity in terms of connectance, richness, and interaction strength, so the results seemed to confirm a negative stability-complexity relationship.[46]

One compelling feature of May's result was its generality. Besides requiring the entries of the diagonal be negative, no assumption was made about the coefficients of **A** from (2). In the parameter space representing all possible linear systems, therefore, May's results seemed to demonstrate that stability is

[45] In another respect, May's analysis was narrower than Gardner and Ashby's given that he set diagonal elements of **A** to –1 rather than allowing them to take values on [–1, –0.1].

[46] Besides specifying that complexity increases with species richness, connectance, and mean interaction strength, May (1974) did not explicitly define complexity. Defining complexity as a simple additive or multiplicative function of these three properties (with equal weights) would accord each property equal import in assessing complexity.

exceedingly rare. It remained possible, May (1974, 173) recognized, that actual biological communities primarily inhabit a rare stable realm of parameter space:

> Natural ecosystems, whether structurally complex or simple, are the product of a long history of coevolution of their constituent plants and animals. It is at least plausible that such intricate evolutionary processes have, in effect, sought out those relatively tiny and mathematically atypical regions of parameter space which endow the system with long-term stability.

To address this possibility, May analyzed several common mathematical models of communities. Two patterns emerged. First, generalizations of simple models representing few species, such as one-predator, one-prey Lotka-Volterra models, to more complicated *n*-species models were generally less likely to be stable than the simple models. This underscored Goodman's (1975) criticism of the first type of evidence Elton (1958) cited in favor of a positive stability-diversity relationship (see §2) because it seemed to show multi-species predator-prey models are generally less, rather than more, stable than predator-prey models of fewer species.

Second, many modifications that made models more realistic also made them less stable. For instance, community models often unrealistically assume an unvarying deterministic environment and thereby set parameters to constant values. May showed that if some or all parameters are allowed to vary stochastically to represent environmental fluctuation, the resulting model is generally less likely to be stable. Similarly, most community models represent birth and death as continuous processes, even though their occurrences are

discrete events in nature. May (1974, 29) found that that more realistic models with discrete variables are likely to be less stable than their continuous counterparts, as well as chaotic dynamics from relatively simple models (May 1976).[47] The disparity between models with discrete and continuous variables also becomes more pronounced as the number of variables increases.

The upshot of May's work was that stability is rare both in the "parameter space" of possible models and for more realistic community models, and that its probability decreases with model complexity. What it showed about actual biological communities, as opposed to models of them, remained unclear. Lewontin (1969) had argued, for instance, that the relationship between local stability and ecological stability is tenuous at best (see §3).[48] May's analysis could therefore be an interesting mathematical exercise with little or no biological application. For this reason, in fact, May (1974, 75-76) hedged about the proper interpretation of his results: "the balance of evidence would seem to suggest that, in the real world, increased complexity *is* usually associated with greater stability." Thus, for May, the results "suggest that theoretical effort should concentrate on elucidating the very special and mathematically atypical sorts of complexity which could enhance stability, rather than seeking some (false) 'complexity implies stability' general theorem" (1974, 77). May recognized that

[47] Surprisingly, May (1976) also found that these simple difference equations sometimes exhibit chaotic dynamics.

most natural biological communities may have evolved a specific structure (the "atypical complexity") that generates stability. For May, what this structure is should be the focus of ecological modeling.

On the methodological details of May's approach to the relationship between complexity and stability, furthermore, some ecologists were unconvinced. Given the myriad of systems that can be randomly constructed using his methodology, *e.g.* 10^{764} for systems with 40 variables, and the "miniscule fraction" of those that represent biologically realistic systems, Lawlor (1978, 446) argued that, "it is extremely unlikely that any of the random systems generated by May and analyzed in terms of their eigenvalues even remotely resemble biologically acceptable ecological systems."[49] DeAngelis (1975) took this argument a step further and showed that for systems constructed according to several biologically plausible principles – that the assimilation efficiency of predator-prey interactions is less than 100%; that some species have a tendency to increase near equilibrium in the absence of interactions with other species (true of some autotrophs), *etc*. – the probability of stability actually increases with increasing connectance.

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[48] Chapter 4 considers the question of the relationship between ecological stability and Lyapunov stability, local, asymptotic, global, *etc*. in detail.

[49] Lawlor calculated the proportion of the total set of randomly constructed systems that were biologically realistic by determining the fraction that exhibited certain biologically plausible properties, such as having no more than 5-7 trophic levels, no food chain loops, or having at least one producer.

Despite May's (1974) qualifications and these criticisms, his work was widely accepted (Lawlor 1978) and taken to overturn the consensus about a positive correlation between community complexity and stability in favor of a negative one (DeAngelis 1975). Earlier work on the SDC debate, however, did not concern the relationship between local stability and complexity, which was May's main focus. MacArthur (1955), Elton (1958), and Pimentel (1961), for instance, whose work set most ecologists' initial expectations about the debate, were concerned with resistance and constancy, not local stability, and focused primarily on species richness rather than complexity. May's analysis only provides insights into the stability-diversity relationship, therefore, if local stability and ecological stability (despite Lewontin's [1969] objections) and ecological diversity and complexity are closely related. Diversity and complexity are related in the weak sense that species richness is a component of both, but this relationship is too weak to guarantee even that a positive correlation between them exists.

Figure 1. Example of the graphical technique for evaluating stability of predator-prey interactions from Rosenzweig and MacArthur (1963).

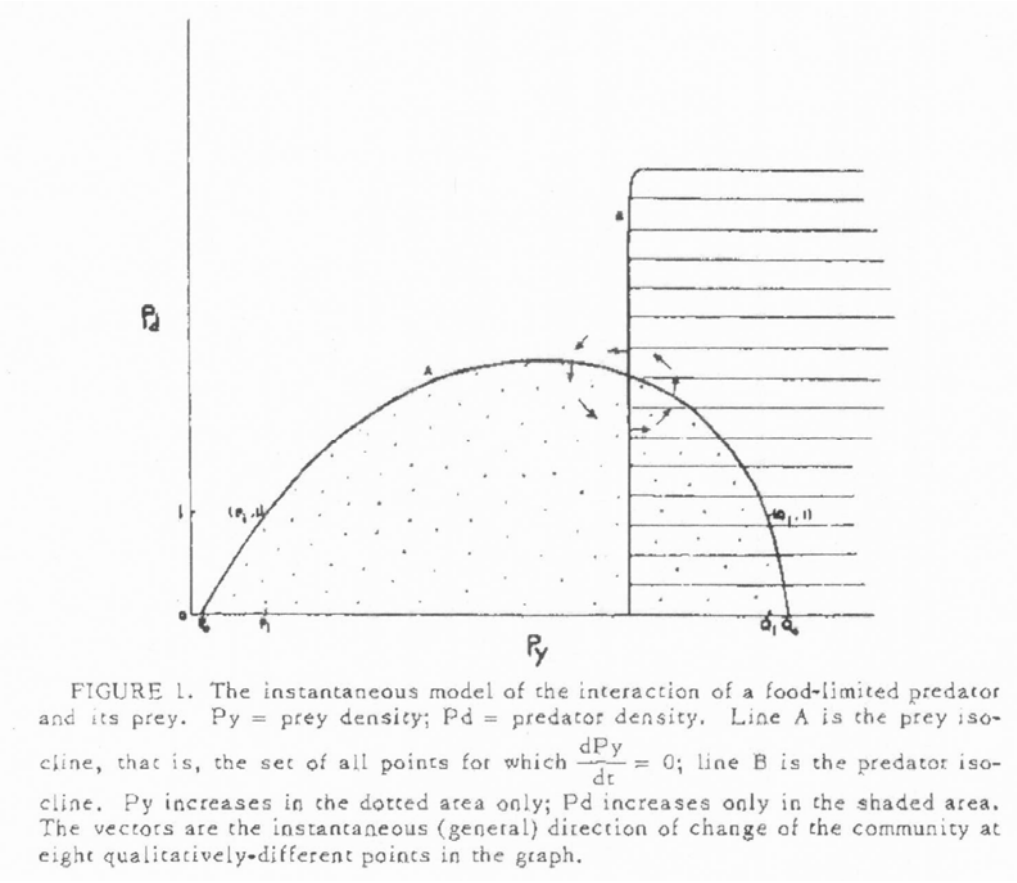

FIGURE 1. The instantaneous model of the interaction of a food-limited predator and its prey. Py = prey density; Pd = predator density. Line A is the prey isocline, that is, the set of all points for which $\frac{dPy}{dt} = 0$; line B is the predator isocline. Py increases in the dotted area only; Pd increases only in the shaded area. The vectors are the instantaneous (general) direction of change of the community at eight qualitatively-different points in the graph.

CHAPTER 3: EXPLICATIVE DEFINITION: A DEFENSE

1. **Introduction**.

The problem of defining concepts – ecological stability, diversity, and complexity – is at the core of the stability-diversity-complexity (SDC) debate. Part of the problem concerns how these three *particular* concepts should be defined. What properties of biological communities are they intended to capture and why? What definitions would accurately represent these properties and what form should they take? Can concepts developed in other scientific contexts (*e.g.* information theory and physics) help formulate such definitions? Adequately defining these concepts requires careful evaluation of these and other specific issues, which Chapter 4 undertakes for ecological stability and Chapter 5 undertakes for ecological diversity and complexity. This task raises a more fundamental issue, however, about how concepts should be defined. Specifically, what adequacy criteria should definitions found in science and philosophy, opposed to a dictionary, satisfy? This chapter attempts to answer this question.

There are disagreements about the appropriate answer to this question, and they reflect fundamentally different views of the purpose of definition, and philosophical analysis in general. The main divergence about definition concerns the relationship between the meaning of the *definiendum* (the concept being defined) and its *definiens* (the concept(s) doing the defining). Should they be strongly similar, for instance extensionally identical or perhaps intensionally very

similar, or may the relationship be weaker? Rudolf Carnap (1950) answered this question in favor of a weaker relationship, and Section 2 sets the context of the debate about definition by describing his account of 'explication', Carnap's technical term for definition. This conception of definition underlies, for instance, Millikan's (1989) "theoretical definition" of the concept of function and Dowe's (2000) "empirical analysis" (rather than conceptual analysis) of the concept of causation.

Carnap (1950) presented explications of some simple empirical concepts, but the primary emphasis there and throughout his career was the explication of theoretical concepts such as analyticity, degree of confirmation, semantic information, *etc*. (*e.g*. Carnap 1937, 1947, 1950; Carnap and Bar-Hillel 1953). Section 3 illustrates Carnap's most important adequacy criteria for explication – precision, fruitfulness, and similarity between the concept being explicated (the *explicandum*) and those providing the explication (the *explicata*) – with respect to the explication of a complex empirical concept, ecological stability.[50] Different definitions of this concept proposed in the ecological literature show how these criteria can be satisfied in different ways, and this section also suggests priority relations between the criteria.

[50] Carnap suggested another adequacy criterion, simplicity, but emphasized that its import was secondary to precision, fruitfulness, and similarity (1950, 7).

Section 4 considers P. F. Strawson's (1963) criticisms of explication. His main objection was that Carnap's similarity criterion is too weak. Without strong similarity, perhaps even synonymy between *explicandum* and *explicata*, Strawson (1963, 505) argued that Carnapian explication is "utterly irrelevant" to the goal of philosophical clarification of concepts. Carnap, on the other hand, was willing to sacrifice strong similarity to increase precision or fruitfulness with an explication. Their disagreement therefore turned on the relative import of different adequacy criteria for definition, specifically similarity vs. precision and fruitfulness.

This disagreement about how definitional adequacy should be assessed, Section 5 argues, stems partly from different views of the purpose of definition and partly from disagreements about what best achieves those purposes. Definitions found in philosophical contexts often attempt to maximize intuitive similarity with the imprecise concept being defined (DePaul and Ramsey 1998) – usually an ordinary concept of natural language that philosophical scrutiny has shown to be problematic in some way – in an attempt to clarify and systematize relations between these and other natural language concepts. Analyses of intuitions about these concepts, though they often diverge significantly among philosophers (REFs), are therefore assumed to provide the main guidance about definitional content here.

Definitions within scientific contexts, on the other hand, often sacrifice intuitive accord with the imprecise concept being defined to enhance formal rigor,

experimental testability, measurability in the field, theoretical unification, integration with well-developed mathematical theories, *etc*. The objective here is to improve our ability to describe the world by establishing a relationship between concepts used to do this in nonscientific contexts or in previous stages of scientific development, and concepts (ideally of well-confirmed scientific theories) that provide the best or at least a better description of the world thus far. In other words, definitions should help facilitate in discovering the structure of the world, which is not reliably achieved by inspecting intuitions, at least according to recent criticisms (*e.g*. Harman 1994; Cummins 1998; Goldman and Pust 1998; Hintikka 1999).[51] Given this goal, definitions should be judged according to how they contribute to scientific practice – in helping generate predictions for instance – because science, rather than philosophical intuition, has best accomplished this goal. This was the principal motivation underlying Carnap's conception of explication.

Strawson (1963, 1992) and others (*e.g*. Moore 1942; Sorenson 1991), however, regard definitions as the end products of conceptual analysis in which intuitions provide the primary guidance, and therefore *should* play the main role in constructing and evaluating definitions.[52] This view of definition, or at least the

[51] The idea that some concepts better help describe the structure of the world than others should not be taken to presuppose some type of scientific realism. 'Better description' could be evaluated in terms of empirical adequacy or the generation of new technologies, for instance, by antirealists.
[52] "Paradigmatic conceptual analyses offer definitions of concepts that are to be tested against potential counterexamples that are identified via thought experiments" (Margolis and Laurence 2006, §2.1).

idea that intuitions should play some nontrivial role in the formulation of definitions, is unproblematic if the definitional goal is simply to clarify the meanings of ordinary concepts of natural language.[53] Besides intuitions, linguistic studies of how words are actually used by speakers of natural language (Jackson 1998), and studies of the mental representation of concepts in the cognitive sciences (Goldman and Pust 1998) also help achieve this goal. The results of such studies therefore could (and should) inform the defining process on this view. If the purpose of the definition is to improve our conceptual framework's ability to describe and determine what the world is like, however, Section 5 argues this conception of definition is indefensible.

2. **Carnapian Explication**.

One of the most sophisticated philosophical discussions of definition is found in the first chapter of Carnap's (1950) *Logical Foundations of Probability*. The chapter's objective was a preliminary clarification of the nature of

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[53] This analysis presupposes no account of what concepts or meanings are. The claim that intuitions may help clarify the meanings of natural language concepts does not, therefore, entail they or their meanings exist as mind-independent intensional objects, or that a clear distinction between a concept's intension and extension is defensible. As empirical evidence about how competent natural language speakers understand and employ terms of a language (see §5.1), even a deflationist about meaning such as Quine could thereby recognize the role intuitions could have in developing a better scientific account of the linguistic activity of humans (see Quine 1953; Margolis and Laurence 2003). Despite their disagreement about intentions, moreover, Quine agreed with Carnap about the import of explication within philosophy (Quine 1960, pp. 257-262).

explication, Carnap's technical term for definition,[54] before Carnap explicated the concept 'degree of confirmation' with a logical relation between hypothesis and evidence statements as the basis of a system of inductive logic.

Explication is the transformation or replacement of an imprecise concept (*explicandum*) with a new concept (*explicatum*) or concepts (*explicata*) subject to four adequacy criteria:

(i) similarity (of meaning) to the explicandum;
(ii) exactness;
(iii) fruitfulness; and,
(iv) simplicity.

The first criterion was much weaker than what most philosophers required of definition. Russell's (1919, Ch. 16) theory of descriptions,[55] for instance, required synonymy between a proposition containing a description and the propositions defining it and Moore (1942, 663) required synonymy between a concept and the concept(s) defining it. Carnap, however, only intended the similarity criterion to ensure the explicatum could be used in *most* cases in which the explicandum was normally used; the explicatum was not required to preserve the explicandum's

[54] 'Definition' is being used here in the broad sense that corresponds to Carnap's conception of 'explication.' This is the sense of 'definition' used in discussions of the problem of defining the species concept in biology, for instance (see Ruse 1969; Kitcher 1984; Ereshefsky 2001), and the one recognized by Carnap (1950, 7) in his statement that: "A good explicit formulation is given by Karl Menger in connection with his explication of the concept of dimension ("What is dimension?" *Amer. Math. Monthly*, 50 [1943], 2-7; see p. 5: §3 "Criteria for a satisfactory definition" [*explication, in our terminology*])," emphasis added. When it is unclear from the context, 'explicative definition' (Belnap 1993, 116) is used to specify this sense of definition below.

[55] Incidentally, Russell called his analysis a "theory of descriptions" only once, in the last paragraph of the essay (1919, 180). Throughout the rest of the essay his analysis was characterized as a "*definition* of descriptions" (emphasis added).

meaning exactly. Carnap would probably accept an explicatum that could be used in most of the *important* cases since (i) permitted "considerable differences" (1950, 7) in meaning.[56] Explication is therefore distinct from lexical definition (Loomis and Juhl 2006), which at least in principle requires identity of meaning. It is also distinct from stipulative definition if the stipulation involved is not required to preserve any relationship between meanings (Belnap 1993; *cf*. Loomis and Juhl 2006, 287). Explicative definitions, Belnap (1993, 116) notes, are "perhaps the most distinctively philosophical acts of definition," in which, "one wants both to rely on an *old*, existing meaning and to attach a *new*, proposed meaning."

Why allow such latitude between explicandum and explicatum? For Carnap, sacrificing close similarity was sometimes justified by the increase in fruitfulness afforded by departing from the explicandum meaning. This accorded, Carnap emphasized, with scientific practice. As an example, Carnap discussed how the "prescientific" concept of 'Fish', which roughly meant 'animal living in water' and included marine mammals among its referents, was replaced as a science of zoology emerged by a narrower concept (Piscis) that excluded

[56] Carnap's descriptions of the relationship sometimes suggest that the "similarity" required could be extremely weak. In the example of explicating 'fish', for instance, he says the explicatum and explicandum "do not even approximately coincide," and are, "far remote" (1950, 6). Since this seems to be incompatible with the explicatum being used in the *important* cases in which the explicandum was used, and is certainly incompatible with the claim that it could be used in *most* cases, the similarity criterion will be assumed to preclude such a weak relationship.

mammals. According to Carnap, the reason the original meaning was not retained was that:

> zoologists found that the animal to which the concept Fish applies, that is, those living in water, have by far not as many other properties in common as the animals which live in water, are cold-blooded vertebrates, and have gills throughout life. Hence the concept of Piscis defined by these latter properties allows more general statements than any concept defined so as to be more similar to Fish; and this is what makes the concept Piscis more fruitful. (Carnap 1950, 6)

From a contemporary perspective, this example is somewhat outdated since phylogeny, rather than phenotypic similarity is the primary reason mammals are excluded from the concept Piscis today.[57] The example nonetheless illustrates that Carnap (1950, 7) understood the fruitfulness of a concept in terms of how many "universal" statements it helped facilitate. For nonlogical concepts, specifically, Carnap suggested fruitfulness be gauged by how many law-like generalizations the explication makes possible; for logical concepts, logical theorems.[58] Explicative definition therefore violates the "conservativeness" or "noncreativeness" criterion commonly invoked in theories of definition within formal languages: a definition should not extend the set of theorems (other than those involving the defined concept) derivable within the language (see Rantala 1991; Belnap 1993).

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[57] See Ereshefsky (2001) for a detailed discussion of this issue.

[58] Frege, Carnap's teacher at Jena in the 1910s (Carnap 1963c), shared the view that definitions of logical and mathematical concepts should be judged according to their fruitfulness. Frege (1980, 100-101) believed definitions should "extend our knowledge" by "drawing boundary lines that were not previously given at all." Logical and mathematical concepts are of course one and the same for a logicist like Frege.

Some philosophically inclined scientists who had considered this issue came to the same conclusion. Lotka (1925, Ch. 1), for instance, argued that exact meaning preservation is secondary to fruitfulness in defining concepts because there is little reason to expect the concepts that have emerged in ordinary language for everyday communication will correspond to the concepts that best describe the world. It may be, he further suggested, that a concept of ordinary language assumed to describe the world in fact has no role to play in its best description provided by science, possibly due to its ambiguity or vagueness. Lotka (1925, 16) suggested this was true of the concepts 'life' and 'causality'.

The most important criterion for Carnap was exactness of the explicatum.[59] Carnap described this criterion as requiring that, "rules of [the explicatum's] use...be given in an *exact* form, so as to introduce the explicatum into a well-connected system of scientific concepts" (1950, 7). Carnap was envisaging the system as a formal language in which explicit meaning postulates and transformation rules specify relations between terms of the language representing concepts precisely, and in which scientific theories are represented by sets of axioms, as described in *Logical Syntax of Language* for instance (Carnap 1937). An explicatum could be introduced into such a language by an explicit definition that would specify relations between it and concepts designated

[59] Carnap (1963, 936) called it "the only essential requirement" in his reply to Strawson (1963). 'Precision' and 'exactness' will be used interchangeably below.

in the axioms, as well as theorems of different theories. Exactness is maximized in this kind of explication, and Carnap (1950, 16-17) cited recursive definition of arithmetical operations with Peano's axioms, and Frege's definition of numerals (1963b, 935) as examples.

The explicatum need not, however, be introduced into such a formal language by an explicit definition. Rather, an explication may simply identify a concept represented in a set of formal axioms as an explicatum for a given explicandum. Satisfaction of the similarity criterion would then depend upon what the axioms say about the explicatum – as interpreted in a model of the axioms – evaluated against the meaning of the explicandum. The explicatum's fruitfulness could be assessed in terms of the theorems entailed by the set of axioms in which it is found. In this case, the nature of the explication of the explicandum depends considerably upon the "implicit definition" the axioms furnish for the explicatum. Muller (2004), for instance, has recently argued that the implicit definition of the set concept furnished by axiomatic set theory provides a highly fruitful explication of the concept.

But as Carnap was well aware, such systematicity is rare among empirical rather than formal sciences. His discussion of exactness for explication of *empirical* concepts correspondingly focused less on integration of an explicatum into an axiomatized theory, and more on making concepts *more* precise, especially through quantification or formalization (see §3). In his reply to

Strawson (1963), Carnap conceded this point explicitly. He (1963b, 935-6) clarified that the exactness criterion only required that the explicatum be more precise than the explicandum, and permitted that the explicatum may belong to a "more exact" part of ordinary rather than formal or scientific language. This constitutes a weakening of his previous claim that an explication should integrate an explicatum into a well-connected system of *scientific* concepts for two reasons. First, the more exact part of ordinary language is presumably more exact because it contains more precise *ordinary* rather than scientific concepts. Two, Carnap believed that relations between concepts of ordinary languages were generally opaque compared to these relations in scientific languages (*cf*. Carnap 1932). To the extent fruitfulness requires precision (see §3), however, the fruitfulness of explications within ordinary language may be limited.

Carnap distinguished three general types of concepts (in order of increasing precision): classificatory, comparative, and quantitative. In the normal progress of science, concepts typically evolve towards greater precision.[60] Carnap (1950, 12) used the concept of temperature as an example. He hypothesized that in an early, undocumented stage in the development of natural language only classificatory concepts like hot, warm, and cold existed. Later, comparative concepts like warmer and colder appeared. Not until science emerged, however,

[60] Carnap was careful to emphasize that the evolution towards concepts with greater precision was typical, not inevitable within science. For example, Carnap (1950, 14) suggested adequate quantitative explicata for some psychological concepts do not exist, and finding comparative explicata should be the focus of explication.

was a quantitative concept of temperature introduced to describe phenomena of heat and cold precisely.

Differences between the quantitative concept of temperature and the comparative concepts of warmer and colder also made clear to Carnap why explication need not ensure that the explicatum can be used in all cases in which the explicandum was used, and thereby preserve meaning exactly. An organism might experience an object to be warmer or colder at two different times due to changes in its physiology even though the quantitative temperature of the object remains constant. Disparities of this kind did not indicate that temperature is an inadequate explicatum for warmer or colder for Carnap because, "we have become accustomed to let the scientific concept overrule the prescientific one in all cases of disagreement" (1950, 12-13). It is certainly true that the scientific concept has supplanted the prescientific one in this case, but Carnap intended the claim to be fully general: if a prescientific concept and its explicatum differ in meaning, the latter takes priority over the former. For Carnap, this was justified by gains in precision and fruitfulness afforded by the explicatum. For Strawson (1963), however, these advantages of the explicatum were irrelevant if its meaning differed from the explicandum, and worse, they were often detrimental to the goal of "philosophical illumination" of the explicandum. This was the basis of Strawson's critique of explication and the focus of Section 4.

The remainder of this chapter focuses on the precision, fruitfulness, and similarity criteria. For the sake of completeness, it should be noted that simplicity was subsidiary to the other three adequacy criteria for Carnap. Carnap (1950, 7) correctly pointed out that many important concepts that are fundamental components of well-confirmed scientific theories are quite complicated, so simplicity should only be a consideration when deciding between explicata of roughly the same precision, fruitfulness, and similarity to the explicandum. The utility of simplicity in explication is therefore context-dependent for Carnap, similar to the context-dependent view of the utility of simplicity in scientific explanation held by Sober (1988).

3. **Adequacy Criteria for Explicative Definition: Precision and Fruitfulness**.

Before considering Strawson's critique, this section illustrates Carnap's adequacy criteria for proposed definitions of a complex empirical concept. Specifically, two common, but very different definitions of the concept of ecological stability show how his exactness and fruitfulness criteria can be satisfied in distinct ways.

The first definition is frequently found in mathematical modeling in ecology (*e.g.* May 1974; Goh 1977; Hallam 1986; Logofet 1993; Kot 2001; Rozdilsky and Stone 2001). Let a vector $\mathbf{x}(t)$ (t designates time) represent an

ecological system like a biological community and let $\mathbf{x}^*$ represent the system at equilibrium.[61] The system at equilibrium is *Lyapunov* stable if and only if:

(1) $$(\forall \varepsilon > 0)(\exists \delta > 0)(|\mathbf{x}(t_0) - \mathbf{x}^*| < \delta \Rightarrow (\forall t \geq t_0)(|\mathbf{x}(t) - \mathbf{x}^*| < \varepsilon)),$$

where ε and δ are real numbers, $\mathbf{x}(t_0)$ represents the system at some initial time t_0, and '$|\cdot|$' designates a Euclidean distance metric. Informally, (1) says $\mathbf{x}^*$ is Lyapunov stable if systems beginning in a neighborhood of $\mathbf{x}^*$ remain near it after being perturbed to the state $\mathbf{x}(t_0)$ at t_0.

The second definition of ecological stability is more frequently found in recent empirical studies of stability-diversity-complexity relationships (*e.g.* Tilman 1996, 1999; Johnson *et al*. 1996; Lehman and Tilman 2000; Cottingham *et al*. 2001). Let B_i be a random variable designating the biomass of species *i* in an *n*-species community *C* assayed during some time period, and let $\overline{B_i}$ designate the expected value of B_i for the time period it is assayed. Tilman (1996, 1999) defined the "temporal stability" of C, $S_t(C)$, as:

(2) $$S_t(C) = \frac{\sum_{i=1}^{n} \overline{B_i}}{\sqrt{\sum_{i=1}^{n} Var(B_i) + \sum_{\substack{i=1;\, j=1 \\ i \neq j}}^{n} Cov(B_i, B_j)}},$$

[61] The components of $\mathbf{x}(t)$ are variables that usually represent densities, abundances, or biomasses of species in the community. Components of $\mathbf{x}^*$ therefore represent these densities, abundances, or biomasses at equilibrium.

where *Var* designates variance and *Cov* designates covariance. Unlike the last definition, S_t defines ecological stability in terms of the variability of biomasses of species in the community. The motivating intuition for this definition is the idea that if two series of abundances are plotted across time, the more stable one exhibits less fluctuation (Lehman and Tilman 2000).

Both definitions satisfy the exactness criterion by eliminating the vagueness of the concept of ecological stability in favor of a precise explicatum, but they do so in different ways. The first definition increases precision by proposing that the formal statement (1) is necessary and sufficient for ecological stability. Alternatively, if ecological stability is understood as a matter of degree rather than dichotomous (as it should be, see Ch. 2, §3), it also seems to be definable within the mathematical framework developed for Lyapunov stability (see Ch. 4, §2). The second definition, on the other hand, increases precision by proposing that ecological stability is a quantitative property of a community whose value is determined by the mathematical function (2).

Although explication requires increasing precision, the epistemic value of explication does not derive from precision itself. Rather, increasing precision is required because it usually enhances fruitfulness. Vague concepts are rarely if ever components of the type of law-like universal statements that were the target of Carnap's fruitfulness criterion. The problematically vague concept 'cause', for instance, is not a technical term of contemporary science (Dowe 2000) and

currently plays no role in any recognized scientific theory.[62] The same can arguably be said of concepts like 'life', 'germ', or 'natural kind.' Making a concept more precise, on the other hand, often facilitates in the development of such law-like statements, as Carnap's simple examples of 'fish' and 'temperature', and the precise characterizations of 'energy' that emerged in mechanics and electrodynamics illustrate. Without sufficiently precise concepts, for instance, it becomes difficult or impossible to derive predictions from sets of statements containing them. Without such predictions, in turn, the sets of statements containing them cannot be confirmed or disconfirmed. Since testing predictions of hypotheses and theories against data is a staple of scientific methodology that the history of science has obviously proved to be an epistemically reliable basis for making inferences, and precision facilitates the use of this methodology, the exactness criterion is therefore justified on inductive grounds.

Although increasing precision has usually enhanced fruitfulness, in some cases it may not, as Carnap noted was the case for some psychological concepts.[63]

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[62] The qualifiers 'contemporary' and 'currently' are intended to grant that the concept could have some such role in the future. Salmon (1997) and Dowe's (2000) account of causal interactions as intersections of world lines that involve exchange of conserved quantities like momentum and energy constitutes a promising candidate among extant analyses of causation. The reason it does is that the account offers a characterization of the concept precise enough to make possible, for instance, its empirical detection, and even empirical measurement of the strength of causal interaction. The concept of causation analyzed by Clark Glmour *et al*. in studies of Bayes net is also promising for the same reasons (see Spirtes *et al*. 2001 for a review).

[63] See footnote 52. Two cases of greater precision not producing greater fruitfulness should be distinguished. It may be that increasing precision does not *now* enhance fruitfulness given the *current* state of scientific knowledge. The law-like statements more precise explicata make

Since there are serious doubts, moreover, about whether law-like generalizations have been discovered in canonical sciences like biology and psychology, the notion of fruitfulness should be broadened to recognize the improvement an explicatum can have in enhancing experimental testability, measurability in the field, theoretical unification, mathematical rigor, *etc*. rather than just in the production of law-like generalizations.

Since (1) and (2) increase precision in different ways, they are fruitful in different ways. The first integrates the concept of ecological stability into a well-developed mathematical theory that provides analytic methods for evaluating the stability of mathematical models of biological communities (see Ch. 4, §2.4). This increase in mathematical rigor, however, has a significant cost. Highly accurate mathematical models describing the dynamics of communities are usually not available. Without such models, evaluation of whether (1) holds must be done with time series data on the variables of $\mathbf{x}(t)$, which is extremely difficult. Strictly speaking, for instance, the universal quantification in the consequent of (1) $[\forall t \geq t_0]$ requires monitoring of the system behavior over indefinite time periods. Another difficulty is that whether (1) holds depends on the behavior of the system after one perturbation (represented by the displacement from $\mathbf{x}^*$ to $\mathbf{x}(t_0)$), but

possible may just fail to be recognized by scientists at given time. Greater precision does not produce greater fruitfulness in a stronger sense, however, if what the concept being explicated represents is essentially imprecise to some degree. Beliefs states of humans, for example, may be best described with imprecise, rather than fully quantitative probabilities (Walley 1991, Ch. 5). In this case greater precision may not increase, and even decrease fruitfulness due to facts about the world, rather than just limitations of scientists' epistemic acumen (see Justus 2006).

empirical evaluation of this behavior in the field can be obscured when, as is often the case, the environment frequently subsequently perturbs the system.

In fact, the infeasibility of empirical evaluation of (1), was one of the advantages Lehman and Tilman (2000, 535) cite in favor of (2). They suggest temporal stability is "readily observable in nature" because evaluation of (2) only requires empirical measurement of biomasses, rather than the difficult empirical assessment of system behavior required by (1). Greater measurability with (2), however, also comes at a cost. Unlike Lyapunov stability, temporal stability has no theoretical underpinning in a mathematical theory of system dynamics (see Ch. 4, §2). (2) also does not define ecological stability in terms of how a biological community responds to perturbation, which seems to be an indispensable feature of the concept, and therefore threatens to violate the similarity criterion as well as the fruitfulness criterion (see Ch. 4, §1.3). Ideally, one would like an explication to enhance all types of fruitfulness while retaining sufficient similarity to the explicandum, without tradeoffs. The tradeoffs in fruitfulness between (1) and (2), however, indicate that this may be rare within science.[64]

(1) and (2) therefore define ecological stability in different, nonequivalent ways. Lyapunov stability, for instance, is a dichotomous concept whose application requires a community initially be at equilibrium, whereas temporal

[64] The most plausible candidates are probably definitions of concepts that are part of well-confirmed, mathematical, and quantitative theories in physics, such as the concept of energy in mechanics or entropy in thermodynamics.

stability is a matter of degree and places no restrictions on the initial state of the community.[65] The existence of nonequivalent definitions for the same concept would typically be taken to indicate an underlying ambiguity of that concept. Chapter 4 argues that the concept of ecological stability has three components, so this multifacetedness may account for the disparity between (1) and (2).[66] In general, however, the existence of multiple, distinct explicata for an unambiguous explicandum is permissible on Carnap's account of explication (Loomis and Juhl 2006, 288). Since preservation of strong similarity of meaning is not required, different explicata can be proposed that differ from the meaning of the explicandum in distinct ways. Pursuing several distinct explications for a given explicandum may even be useful since different explicata could be fruitful in distinct ways, similar to exploring the merits of different logics (*e.g.* Carnap 1937). It was this permissive view of the relationship between the meaning of the explicatum and explicandum, however, that prompted Strawson's criticism of explication.

4. **Strawson's Criticism**.

As a method of conceptual clarification, Carnap placed no restriction on the scope of application of explication. It was intended to help clarify concepts of

[65] Chapter 4 discusses differences between the concepts in detail.

[66] Chapter 4 also argues that neither (1) nor (2) adequately define ecological stability.

the empirical and formal sciences, as well as those found in ordinary language and philosophy. Explication contrasts sharply, however, with another method of conceptual clarification adopted by P. F. Strawson (1963, 1992) and widely utilized and defended within contemporary analytic philosophy (*e.g*. Sosa 1983, 1998; Bealer 1996a, 1996b, 1998). Instead of searching for a suitable explicatum for an imprecise explicandum or constructing an entire artificial system of precise explicata to clarify a set of ordinary concepts of natural language, Strawson (1963, 514-518) advocated trying to determine the underlying principles assumed to govern the use of these concepts in everyday communication, or the principles that would govern their use in a highly idealized, maximally rational and philosophically informed version of this communication. Finding such principles would clarify the underlying "logical" nature of these concepts, and supply the best basis for a philosophically defensible definition of them. Consequently, Strawson believed this method, not explication, provided the best way to resolve philosophical problems and confusions generated by these concepts. For the sake of brevity and to distinguish it from explication, call this method 'conceptual analysis.'

With this method of conceptual clarification in mind, Strawson's main criticism of explicative definition was that it is not "philosophically illuminative":

> however much or little the constructionist technique [*i.e*. explication] is the right means of getting an idea into shape for use in the formal or empirical sciences, it seems prima facie evident that to offer formal explanations of key terms of scientific theories to one who seeks philosophical illumination of essential

> concepts of non-scientific discourse, is to do something utterly irrelevant–is a sheer misunderstanding, like offering a text-book on physiology to someone who says (with a sigh) that he wished he understood the workings of the human heart. (Strawson 1963, 504-505)

Part of his basis for this claim was the observation that:

> it seems in general evident that the concepts used in non-scientific kinds of discourse could not literally be *replaced* by scientific concepts serving just the same purposes; that the language of science could not in this way *supplant* the language of the drawing-room, the kitchen, the law courts and the novel. (Strawson 1963, 505)

Since nonscientific concepts cannot be replaced by scientific ones and retain the same functionality, there is no reason to expect a "well-connected system" of the latter would shed any light on the former. It follows, Strawson asserted, "that typical philosophical problems about the concepts used in non-scientific discourse cannot be solved by laying down the rules of exact and fruitful concepts in science. To do this last is not to solve the typical philosophical problem, but to change the subject" (1963, 506). Instead of providing insights about concepts that generate philosophical puzzles, explication pursues the project of finding precise substitutes for them, thereby abandoning the only subject matter that he believed could help resolve the puzzles. The philosophical illumination furnished by explication is therefore negligible.

Strawson located Carnap's motivation for explication, as opposed to conceptual analysis of ordinary language, in an untenable, even dogmatic (Strawson 1963, 517) dismissal of traditional philosophical problems. For Strawson, if explicata are to provide any insights about the concepts (explicanda)

that generate philosophical puzzles, a clear account of the relations between the two is necessary. Such an account is only possible, however, with an accurate description of the explicanda, as would be provided by the type of conceptual analysis Strawson endorsed. One could only think otherwise, Strawson (1963, 513) suggested, "if one is led away from the purpose of achieving philosophical understanding by the fascination of other purposes, such that of getting on with science."

The alternative to explication is careful analysis of the ordinary concepts of natural language that generate philosophical problems and confusions themselves. As an instance or end product of conceptual analysis, the goal of definition for Strawson was thus the elucidation of the underlying nature of the concepts being defined. This elucidation would resolve or at least help clarify any philosophical puzzles generated by these concepts. The way these concepts are used in everyday communication, intuitions about them, and thought experiments that probe the limits of their range of defensible application would provide the raw material from which the elucidation is derived. Judicious scrutiny of these factors would uncover the "logical behavior which ordinary concepts exhibit" (Strawson 1963, 513) that may be masked by the "elusive, deceptive modes of functioning of unformalized linguistic expressions" (1963, 512). Strawson (1992, 7) later clarified this conception of conceptual analysis with an analogy:

> Just as we may have a working mastery of the grammar of our native language, so we have a working mastery of [our] conceptual equipment. We know how to

> handle it, how to use it in thought and speech. But just as the practical mastery of the grammar in no way entails the ability to state systematically what the rules are which we effortlessly observe, so the practical mastery of our conceptual equipment in no way entails the possession of a clear, explicit understanding of the principles which govern our handling of it, of the theory of our practice. So – to conclude the analogy– just as the grammarian, and especially the model modern grammarian, labours to produce a systematic account of the structure of rules which we effortlessly observe in speaking grammatically, so the philosopher labours to produce a systematic account of the general conceptual structure of which our daily practice shows us to have a tacit and unconscious mastery.

On this view of conceptual analysis, it is clear why it is imperative that definitions faithfully preserve and not distort the current meaning of concepts. Only with an exact account of the actual meaning of ordinary concepts of natural language is it possible to elicit their supposed underlying structure and potentially resolve any philosophical puzzles they generate. That more precise explicata for these concepts can be formulated that possess the virtues Carnap extolled is therefore irrelevant to the proper function of definition within philosophy.

5. **Definition and Philosophical Method**.

The fundamental disagreement between Carnap and Strawson about definition concerned the similarity criterion. Carnap was willing to sacrifice close similarity between explicatum and explicandum to achieve greater precision and fruitfulness with the former. For Strawson, to the extent one deviates from the meaning of the explicandum, one abandons the goal of philosophically illuminating concepts in favor of another, replacing them.

5.1. Common Ground.

It is important to recognize that Carnap could agree with Strawson about one aspect of this issue: construed as an *empirical* method of inquiry about concepts, conceptual analysis can help clarify the actual meanings of ordinary concepts. Exploiting Strawson's (1992) analogy (see §4), just as a linguist analyzes the linguistic practices of speakers of natural languages in an attempt to determine their syntax and semantics, a philosopher can analyze how concepts are used in an attempt to identify their meanings and elucidate relationships between them. Moreover, how terms of natural language that designate concepts are used in everyday communication can help pinpoint these meanings and relationships.[67] Linguistic studies of how terms are used (Jackson 1998), as well as studies of the mental representation of concepts in the cognitive sciences (Goldman and Pust 1998; Ramsey 1998), should therefore play an important role in conceptual analysis understood in this empirical sense. In fact, Carnap (1963a, 920) explicitly advocated this kind of empirical approach to determining meaning:

> It seemed rather plausible to me from the beginning that there should be an empirical criterion for the concept of the meaning of a word or a phrase, in view of the fact that linguists traditionally determine empirically the meanings, meaning differences, and shifts of meanings of words, and that with respect to these determinations they reach a measure of agreement among themselves…In [Carnap 1955], I tried to show the possibility of giving operational rules for testing hypotheses concerning the intensions of predicates of a natural language, on the basis of responses by the users of this language.

[67] This assumes a weak version of the use theory of meaning: the way terms of natural language are typically used provides reliable information about (but does not necessarily determine) their meaning, and the meaning of the concepts they designate (see Wittgenstein 1953).

'Intension' is Carnap's technical term for the meaning of a predicate. This passage and the method for determining predicate intensions in natural languages developed by Carnap (1955) were responses to Quine's criticisms of the analytic-synthetic distinction. If intensions can be determined using this method, it is plausible statements concerning these intensions, such as 'All bachelors are males,' can be identified as analytic. Given their disparate philosophical commitments, the significant congruence in Carnap and Strawson's response to Quine's criticisms is striking (*e.g.* Grice and Strawson 1956).

This type of empirical conceptual analysis has a natural place in Carnap's account of explication as a means of "clarifying the explicandum" (Carnap 1950, 3-5). Before proposing an explicatum for an explicandum, Carnap stressed that the meaning of the latter should be clarified as much as possible through informal methods. This preliminary clarification would help determine whether the explicandum is ambiguous, in which case more than one explicatum would be appropriate, or whether the meaning of the explicandum is too vague to even be explicated.[68] If an explicandum is too vague, presumably its similarity to potential explicata cannot be evaluated, and attempts to explicate it would therefore be pointless.[69] Carnap (1963b, 936) allowed, furthermore, that the analysis of

[68] "[Philosophers] often immediately start to look for an answer [to questions like 'What is *X*?' where *X* is some concept] without first examining the tacit assumption that the terms of the question are at least practically clear enough to serve as the basis for an investigation, for an analysis or explication" (Carnap 1950, 4).

[69] Carnap (1950) did not make this argument explicitly.

ordinary language may sometimes be sufficient to resolve some philosophical confusions that emerge when terms of ordinary language are used outside their normal contexts in everyday communication.

Carnap could even grant that proverbial "armchair" conceptual analysis – in which philosophers focus on what their intuitions about concepts reveal about them – helps clarify the actual meaning of ordinary language concepts. Philosophers are (usually) competent speakers of natural languages and are also usually especially keen to subtle differences in meaning, so their understanding of a concept at a minimum counts as relevant empirical data about its meaning (Goldman and Pust 1998; Graham and Horgan 1998). Since philosophers' intuitions about concepts will likely reflect their philosophical commitments involving them, however, it is unlikely their intuitions will agree (because their commitments often diverge) or that their intuitions will reflect those of the general populace (because the populace arguably does not share most of these commitments) (Dowe 2004).

5.2. **The Epistemic Limitations of Intuition**.

Despite their potential accord on these points, "clarification of the explicandum" was only intended as a preparatory step before explication. Although Carnap could endorse attempting to determine the exact meaning of the explicandum with the methods considered above as a pre-explication preliminary,

explication allowed departure from the actual meaning of the explicandum, and this was the core of the disagreement between Carnap and Strawson.

As Section 4 made clear, Strawson's criticism of explication was based on a more substantive conception of conceptual analysis than discussed above (§5.1). This view of conceptual analysis and the conception of definition that accompanies it are commonly found within contemporary analytic philosophy (*e.g.* Sosa 1983, 1998; Bealer 1996a, 1996b, 1998).[70] Conceptual analysis is taken to be something more than an empirical inquiry into what individuals trained in philosophy introspect about the meaning of concepts. Results of such inquiries, and definitions built upon them, would seem to lack any normativity; they would merely *describe* the way a fairly small set of individuals (likely unrepresentative of the general populace) understand certain concepts, not *prescribe* the way those concepts should be understood.

Rather than accept this attenuated view, the intuitions about concepts appealed to in such analyses are considered to have a special status: "[conceptual analysis] attempts to show the natural foundations of our logical, conceptual apparatus, in the way things happen in the world, and in our own natures"

[70] One prominent exception is Jackson (1998, 44), who is "suspicious" about the view that conceptual analysis provides insights about the world. He calls this "immodest" conceptual analysis, and expresses doubts about his earlier use of it in the knowledge argument (*e.g.* Jackson 1986). Jackson (1998) defends instead a "modest" conceptual analysis that merely attempts to determine the folk theory he assumes underlies the use of ordinary concepts in natural language. If this is the goal, however, it is unclear what legitimate role modest conceptual analysis has, as Jackson believes it does, in metaphysics which, as traditionally understood, is concerned with uncovering the fundamental nature of the world (*cf.* Jackson 1998, Ch. 3).

(Strawson 1963, 516). The purpose of conceptual analysis is therefore to uncover the "foundation of our concepts in natural facts, and to envisage alternative possibilities, it is not enough to have a sharp eye for linguistic actualities" (1963, 517).[71] A definition of a concept should accordingly reveal its connections to other concepts as determined by intuitions about this "natural foundation," and it is this foundation that supplies a definition with prescriptive force. Deviation from intuitions about meaning for the sake of increasing precision or enhancing fruitfulness, regardless of how epistemically useful this has proved to be in the past, is therefore indefensible. For this reason, definitions developed on the basis of this kind of conceptual analysis have been identified with the now out of favor notion of a "real definition" in which the intended goal was to capture the alleged "essence" of the concept being defined (Anderson 1993, 200).[72]

There is an obvious question to raise about this view of conceptual analysis and the conception of definition that accompanies it. What, if anything, do intuitions about concepts demonstrate beyond merely how a set of humans understand and use a particular set of concepts?[73] The remainder of this chapter

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[71] This statement suggests there is a divergence between the structure of our concepts as grounded in "natural facts" about the world, and the conceptual structure underlying our linguistic practices. The statement therefore seems to be in tension with Strawson's (1992) analogy with the grammarian (see §4).

[72] See Robinson (1950, Ch. 6) for a detailed discussion of real definition.

[73] There is another potential problem with Strawson's view of conceptual analysis, which will not be pursued here. Strawson assumed an underlying "system" or "structure" exists that governs our concepts and explains how terms of ordinary language that refer to them are used in everyday communication (1963, 513; 1992, Ch. 2). Unfortunately, Strawson never made clear what the form of this conceptual system or structure was. He did call it "logical" (1963, 513), however, and this seems to suggest conceptual analysis should reveal *logical* relations between concepts, *i.e.*

considers what implications recent compelling criticisms of the epistemic status of intuitions have for how definition should be understood. A comprehensive review of these criticisms cannot be undertaken here, but an appreciation of their consequences for definition requires a clear account of the main weaknesses they reveal about relying on intuitions in philosophical inquiry.

Two goals must be kept distinct in evaluating the epistemic status of intuitions. One, discussed above, is whether intuitions *can* help clarify the meaning of concepts, which there is little reason to doubt (see §5.1).[74] The other, more problematic goal is that intuition provides reliable insights about the world.

Given their poor track record (Harman 1994; Hintikka 1999), the burden of proof is on proponents of intuitions to defend their epistemic utility. Different kinds of attempts have been made to establish this, and the problems with one of the most cogent (Sosa 1998) reveals the fundamental difficulties of the position.

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necessary and sufficient conditions. Whether there is such a structure that governs our concepts is an empirical question. Experiments within psychology, especially those of Eleanor Rosch (*e.g.* Rosch and Mervis 1975), cast doubt on the plausibility of this account as a description of the *actual* conceptual structure possessed by humans. Based on psychological evidence that context-sensitive prototypes govern the use of concepts, for instance, Ramsey (1998) points out that the traditional goal of finding necessary and sufficient conditions that are resistant to intuitive counterexamples through conceptual analysis is indefensible.

[74] There is room for controversy about even the weak claim that intuitions *can help* clarify meanings. If meanings are mental entities, for instance, behaviorists claim that they can only be clarified and explained by agent behavior, not by appeal to other mental events like intuitions. More importantly, there are also serious reasons to doubt that appeals to intuition will be *sufficient* to resolve disputes between incompatible philosophical positions about the proper meaning of some concepts, such as 'free act,' 'cause,' 'personal identity,' 'knowledge,' *etc*. (see Stich 1998; Sider 2001; Unger 2002; Dowe 2005).

Sosa first gives an explicit definition of intuition in terms of inclination to believe:

> At [time] t, it is intuitive to [subject] S that [proposition] p iff (a) if at t S were merely to understand fully enough the proposition that p (absent relevant perception, introspection, and reasoning), then S would believe that p; (b) at t, S does understand the proposition that p. (1998, 259)[75]

With this definition, Sosa then argues that there is a strong analogy between intuitions on the one hand, and perception and introspection on the other. The latter are fallible, prone to serious and sometimes systematic error, even under normal circumstances, and, Sosa (1998, 263) suggests, there is currently no well-developed theory of introspection. Intuition is in the same lot. Sosa mentions well-known paradoxes and the intuitive, but problematic naïve comprehension axiom of set theory as specific examples of the fallibility of intuition, and admits that recent psychological literature shows that, "even in conditions of apparent full normality, with high alertness and ample reflection time, subjects systematically go wrong in their reasoning and the intuitions involved" (1998, 261). Despite their deficiencies, however, perception and introspection are typically and rightly, Sosa contends, relied upon as sources of justified true beliefs. According to the analogy, to the extent perception and introspection are

[75] Sosa (1998, 258) includes the clause that *p* be "abstract" but refrains from defining what it for *p* to be abstract, saying, "our working concept of the concept [of being abstract] seems good enough for present purposes." He clarified, however, that the restriction to abstract propositions was intended to focus on "the sort of intuition that seems important for the armchair theorizing of philosophers," (1998, ff. 1), so 'abstract' has a broad connotation beyond merely logical or mathematical propositions. It includes, for instance, the intuition that space is Euclidean (1998, 258). In any case, Sosa's argument does not depend upon *p* being abstract (see below).

epistemically trustworthy sources of justified true belief, intuition should be similarly trusted.

One virtue of Sosa's argument is that it does not rely on *p* being necessary, any ontological view of what *p* designates, or any commitment to how *S* is acquainted with or "grasps" what *p* designates (1998, 260). The argument therefore avoids contentious issues about the objectivity of necessity, or how what *p* designates generates *S*'s inclination to believe *p*.

Aside from serious worries about the epistemic status of perception and introspection especially (*cf*. Schwitzgebel 2006), there are glaring disanalogies with intuition that Sosa does not address. First, introspection and intuition involve fundamentally different kinds of belief. Intuitions concern beliefs about extra-mental facts or properties of some form, whereas introspections are about subjective conscious states for Sosa (1998, 260). What may warrant the claim that introspections are a source of justified true beliefs *about one's subjective conscious states* –for instance the privileged access the one exhibiting such states has to them– suggests nothing by itself about how intuitions could be a source of justified true beliefs *about extra-mental facts of properties*. Absent a bridge between them, which Sosa does not supply, the proposed analogy is inapt.

The proposed analogy between intuition and perception avoids this difficulty because both involve extra-mental facts or properties, but it suffers from others. *If* perception is considered a source of justified true beliefs, it is for at least

two reasons. One is that perception has an overall strong inductive basis. It has for most humans and organisms of other species provided an effective means for interacting with the external world.[76] The second is that much is known about the physiological and psychological mechanisms underlying perception, and that this understanding can often explain why and how perception is sometimes erroneous. The fact that perception is sometimes misleading does not threaten the belief that it is usually epistemically reliable precisely because errors in perception can be explained by appeal to a theory of the mechanisms that underlie veridical perception (Graham and Horgan 1998). Even if the current understanding of perception falls short of this goal, it seems highly implausible that a "completed" theory of perception would fail to provide such explanations.

Intuition shares neither of these epistemic advantages. With respect to the first point, several critics of intuition have pointed out that its inductive basis is extremely poor (*e.g.* Harman 1994; Cummins 1998; Goldman and Pust 1998; Hintikka 1999). "The history of philosophy," Levin (2004, 195) notes, "abounds with well-known examples of now-abandoned theses that once seemed obvious." Typical examples include Kant's claim that space necessarily has the structure described by Euclidean geometry, the idea of absolute, frame-invariant time and

[76] This claim is uncontroversial, but whether it provides grounds for the claim that perception is a source of justified true beliefs depends on the meaning of 'justification' and 'truth,' and what they are taken to require.

space, or the widely held pre-Gettier intuition that knowledge is justified true belief.

Second, although Sosa avoids contentious issues by not presupposing a particular view of how intuitions yield justified true beliefs, the lack of such an account constitutes a significant difference between the epistemic status of perception and intuition. Without it, there is no defensible way to delineate cases where intuition is erroneous from those where it can be trusted, as there is for perception. Unlike perception, therefore, the fallibility of intuition poses a serious threat to its epistemic status. In addition, this is a particularly pressing problem for intuition because of its poor track record compared with perception.

Sosa's position seems to be that the intuitive appeal of some propositions alone is sufficient to justify believing them. About propositions with intuitive appeal like '2+2=4,' 'no cube is a sphere,' even Descartes' *cogito*, Sosa suggests:

> presumably it cannot be just a coincidence that we are right in believing them. It must be more than a coincidence that, with regard to these facts, we get it right: that we would believe that p only were it so that p. Not only must we be so constituted and positioned, so related to the subject matter, that we *would* get it right, or tend to get it right; in addition, it cannot be just an accident *that* we are now so constituted and related. (1998, 262)

It can be agreed that beliefs about these propositions (possibly excepting the *cogito*) are not accidental without agreeing that this lends any epistemic credence to intuition. Unless a compelling account of how one is "related to the subject

matter" is provided that shows how these beliefs are justified *by intuition*, the idea that it must be intuition is merely a supposition, not a warranted conclusion.[77]

It is unlikely, moreover, that such an account will be forthcoming. What is required, Goldman and Pust (1998) point out, is a convincing explanation of how intuitions, which are mental events of some kind (dispositions to believe for Sosa, for instance), are a reliable indicator of facts about extra-mental objects or properties, whether they are the abstract "universals" Platonists attempt to access or the "natural kinds" supposedly discovered in science. With visual perception, for instance, this is supplied by the causal relationships between the objects being perceived, the light reflected from them, the perceiver's retinas, and the visual cortex. Some details of these relationships and those involved in other types of perception may be currently unknown, but it is clear what kind of connection exists between the extra-mental objects or properties perceived and our perceptions of them. The same, Goldman and Pust (1998) correctly stress, cannot be said for intuition.[78]

5.3. **Against a Strong Similarity Criterion**.

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[77] The idea that intuitive appeal is sufficient to justify belief also has a problematic implication: in cases where intuitions diverge –*e.g*. about free will, consciousness, *etc*.– the disputants would both be justified in their beliefs, even though these beliefs are incompatible. This problem is especially troubling if substantial cognitive diversity, and hence diversity of intuitions, exists across cultures (Stich 1998; Weinberg *et al*. 2001).

[78] Goldman and Pust (1998, 187-188) emphasized, however, that intuitions can provide reliable data about the meaning of concepts, assuming a concept is a "psychological structure or state that underpins a cognizer's deployment of a natural-language predicate" (see §5.1).

Although it is not a comprehensive review of recent criticisms of intuition, the previous subsection illustrates some serious problems with the view that intuition constitutes an epistemically reliable source of facts about the world. Assuming these criticisms are sound, what are the implications for definition? If the definitional objective is simply to clarify the actual meaning of concepts, the prevailing view is unproblematic. Given this goal, definitions are not normative; they are merely intended to elaborate the meanings of concepts as determined by how they are used in ordinary language and conceived of by individuals. Intuitions have a part to play in this undertaking, usually in assessing through thought experiments whether concepts are applicable in various hypothetical scenarios far removed from the everyday contexts in which the concepts are normally employed (see §5.1). The results of such analyses do not definitively determine the meanings of ordinary concepts, however. They must be gauged, for instance, against data on how the concepts are actually used in everyday communication and arguably about how the concepts are cognitively represented.

The critique of intuitions has an important implication for definition, however, if its goal is to provide normative guidance about our concepts by playing a role in helping determine what the world is like. If, specifically, the objective of definition is to help align our concepts with a conceptual structure that better describes and better facilitates in discovering the structure of the world, then the absence of a credible epistemic basis for intuition entails that definitions

need not treat them as strongly binding. In particular, definitions need not preserve intuitive *identity* of meaning between definiendum and definiens. Intuitive *similarity*, assuming it accords with other sources of information about the actual meaning of concepts (see §5.1), must be retained, of course, to satisfy the similarity criterion, but definitions can and should deviate from identity or strong similarity to enhance precision and fruitfulness given the epistemic utility of these properties. Such definitions have a normative purpose and specify what the meaning of a concept *should* be rather than what it *does* mean. In other words, since the conceptual apparatus underlying everyday communication, which partly generates intuitions about the meaning of ordinary concepts, is not epistemically privileged, explicative definitions need not be significantly constrained by it.

Freed from strong constraints imposed by intuitions, definition becomes just another cognitive tool that should be evaluated according to the function it, and the broader conceptual and linguistic structure of which it is a part, is intended to serve. This was the view Carnap (1963b, 938-939) advocated:

> In my view, a language, whether natural or artificial, is an instrument that may be replaced or modified according to our needs, like any other instrument…A natural language is like a crude, primitive pocketknife, very useful for a hundred different purposes. But for certain specific purposes, special tools are more efficient, *e.g.*, chisels, cutting-machines, and finally the microtome. If we find that the pocket knife is too crude for a given purpose and creates defective products, we shall try to discover the cause of the failure, and then either use the knife more skillfully, or replace it for this special purpose by a more suitable tool, or even invent a new one. [Strawson's] thesis is like saying that by using a special tool we evade the problem of correctly using the cruder tool. But would anyone criticize the bacteriologist for using a microtome, and assert that he is evading the problem of correctly using a pocketknife?

For this reason, Strawson (1963, 505) was correct to emphasize that precise concepts like those found in science will probably never replace most of those used in ordinary communication (see §4). Loomis and Juhl (2006, 291) are similarly right to point out in response to Carnap's analogy that, "pocketknives are not replaceable by microtomes for most *ordinary* uses" (emphasis added). The fact that ordinary concepts are sufficient for *ordinary* uses and provide an effective means for *everyday* communication does not, however, entail that they are the best or even adequate conceptual tools for accurate description of the world. If this is the 'specific purpose' to which Carnap alludes above, then transforming our ordinary concepts into more precise and fruitful ones is warranted, even if it requires departing somewhat from the meanings of ordinary concepts.

Loomis and Juhl (2006, 291) raise another, related criticism of Carnap's analogy: "someone who was having trouble using a pocket-knife in an *ordinary* circumstance would not be helped in the least by being shown the workings of a microtome" (emphasis added). Although this is probably usually true, it is unclear it critically reflects on explication and Carnap's instrumental view of language in general. Continuing the analogy, if the pocketknife corresponds to the ordinary concept and the trouble arises in an *ordinary* circumstance –*i.e*. one in which the concept is normally used– then it seems the troubled individual does not understand the actual meaning of the concept and should consult a lexical

definition that elaborates that meaning. If the confusion persists, it is likely the individual is expecting more of the concept than it delivers in ordinary circumstances where it functions unproblematically. The microtome corresponding to the more precise explicatum was, after all, only recommended as a "special tool" invoked for "certain specific purposes."

The claim that definitions intended to provide normative guidance about concepts (rather than describe their meanings) must preserve their current meaning exactly seems to assume that these meanings (especially as determined by intuitions particular philosophers, instead of how most individuals understand the concepts) reflect or reveal something about the structure of the world inaccessible to or independent of science (Bealer 1998). If this view is indefensible as recent criticisms have suggested (§5.2), then it appears there is no reason to require strong similarity between definiendum and definiens, and thus no basis for this criticism of explicative definition.

Chapter 4.

How Should Ecological Stability Be Defined?

One fundamental obstacle to resolving the stability-diversity-complexity (SDC) debate is finding an adequate definition of ecological stability. Numerous definitions and categorizations of the concept have been proposed (Lewontin 1969; Orians 1975; Pimm 1979, 1984, 1991; Grimm and Wissel 1997; Lehman and Tilman 2000) and this plurality has been responsible for much of the confusion and lack of progress in resolving the debate. As part of their argument that ecological theory has failed to provide a sound basis for environmental policy – they believe the SDC debate provides a clear example of this failure – Shrader-Frechette and McCoy (1993) have also criticized that several proposed definitions of ecological stability are incompatible and that the concept is itself "conceptually confused" or "inconsistent."

The first part of this chapter presents a comprehensive taxonomy of distinct concepts of ecological stability. The taxonomy indicates what concepts are compatible and reveals other relationships between them. The first part also argues that the concepts of resistance, resilience, and tolerance jointly provide an adequate definition of ecological stability. Roughly speaking, a community exhibits these concepts to a high degree if it: changes little after being perturbed (resistance); returns rapidly to a reference state or dynamic after being perturbed

(resilience); and will return to that reference state or dynamic after most perturbations (tolerance) (see §1.3). The first part of the chapter ends by rebutting the criticisms of Shrader-Frechette and McCoy (1993).

With the concept clarified, the second part of the chapter argues that the common definition of ecological stability as Lyapunov stability is flawed. This definition pervades mathematical modeling in ecology because it integrates the imprecise concept of ecological stability into a well-developed mathematical theory fruitfully utilized in other sciences. Lyapunov stability theory was developed in dynamical systems theory and has been used in applied mathematics to study several subjects, for instance, mechanics, electrical circuits, and economic systems (Hirsch and Smale 1974; Hinrichsen and Pritchard 2005). Lyapunov stability, however, fails to represent the domain of application of ecological stability adequately. This failure illustrates an important limitation of the theory of Lyapunov stability within mathematical ecology.

1. The Many Senses of Ecological Stability.

1.1. Contextualization and Classification of Ecological Stability.[79]

As the history recounted in Chapter 2 shows, 'stability' has been used to designate several different concepts in ecology. Before considering these concepts

[79] In the following, 'ecological stability' designates stability of a biological community unless otherwise specified, though most of the discussion also applies to the stability of a biological population.

in more detail, it should first be noted that their attribution must be made with respect to two evaluative benchmarks. The first is a system description (*M*) that specifies how the system and its dynamics are represented. The second is a specified reference state or dynamic (*R*) of that system against which stability is assessed. In most ecological modeling, *M* is a mathematical model in which:

(i) variables represent system parts, such as species of a community;

(ii) parameters represent factors that influence variables but are (usually) uninfluenced by them, such as solar radiation input into a community; and,

(iii) model equations describe system dynamics, such as interactions among species and the effect environmental factors have on them.

M therefore delineates the boundary between what constitutes the system, and what is external to it. Relativizing stability evaluations to *M* is a generalization of Pimm's (1984) relativization of stability to a "variable of interest" because stability is assessed with respect to (i)–(iii) rather than a subset of (i).

The specification of *M* partially dictates how *R* should be characterized, and *vice versa*. A biological community, for instance, is usually described as a composition of populations of different species. *R* must therefore reference these populations in some way. For example, *R* is often characterized in terms of the "normal" population sizes of each species. Since ecological modeling in the late 1960s and 1970s was dominated by the development of mathematically tractable

equilibrium models (Holling 1973; Chesson and Case 1986; DeAngelis and Waterhouse 1987), "normal" population sizes were often assumed to be those at equilibrium, *i.e*. constant population sizes the community exhibits unless perturbed. This is not the only possible reference specification, however. A community may be judged stable, for instance, with respect to a reference *dynamic* the populations exhibit. Common examples are a limit cycle –a closed path *C* that corresponds to a periodic solution of a set of differential equations and towards which other paths asymptotically approach (Kot 2001, Ch. 8)– or a more complicated attractor dynamic (Hastings *et al*. 1993). Ecological stability can also be assessed with respect to some specified range of tolerated fluctu ation (Grimm and Wissel 1997). *R* may also be characterized solely in terms of the presence of certain species.[80] Only extinction would constitute departure from this reference state.

The details of *M* and *R* are crucial because different system descriptions – *e.g*. representing systems with different variables or representing their dynamics with different functions– may exhibit different stability properties or exhibit them to varying degrees relative to different specifications of *R*. Specifying *R* as a particular species composition vs. as an equilibrium, for instance, can yield different stability results. Similarly, different *M* can produce different assessments

[80] To illustrate the partial dependence of *M* on *R*, notice that the species referred to in *R* must be part of the system description *M*.

of a system's stability properties. Describing a system with difference versus differential equations is one example (May 1974). May (1976), for instance, showed that the logistic *difference* equation:

$$(1) \qquad N_{t+1} = (1+r)N_t - \frac{r}{K}N_t^2;$$

where t is time; r is the intrinsic growth rate; K is the carrying capacity; and N is the population size, exhibits dramatically different behavior than the logistic *differential* equation. For $r > 0$, the logistic differential equation has an asymptotically Lyapunov stable equilibrium $N^* = K$ (see §2.2). This is also an asymptotically Lyapunov stable equilibrium of the logistic difference equation, but only for $0 < r < 2$. For $2 < r < 2.526$ the system exhibits a 2-period limit cycle. As r increases beyond 2.526 a 4-period limit cycle emerges, and the system exhibits chaotic behavior for $r > 2.692$. Thus, although the logistic differential and difference equations appear to describe very similar dynamics, the seemingly inconsequential choice of representing time as a discrete or continuous variable has a substantial effect on evaluating stability properties of the system.

Details of M and R are also important because they may specify the spatial and temporal scales at which the system is being analyzed, which can affect stability assessments. Systems with low resistance but high resilience, for example, fluctuate dramatically in response to perturbation but return rapidly to their reference state R (see §1.2 below). Low resistance is detectable at fine-

grained temporal scales, but systems may appear highly resistant at coarser scales because their quick return to R prevents detection of fluctuation. Similarly, significant fluctuations in spatially small areas may contribute to relatively constant total population sizes maintained through immigration and emigration in larger regions.

Once (and only once) M and R are specified, the stability properties of a system can be determined. These properties fall into two general categories, depending on whether they refer to how systems respond to perturbation (relative to R) or refer to system properties independent of perturbation response (see §1.2, §1.3). A perturbation of an ecological system is any discrete event that disrupts system structure, changes available resources, or changes the physical environment (Krebs 2001). Typical examples are flood, fire, and drought. Perturbations are represented in mathematical models of communities by externally induced temporary changes to variables that represent populations, to parameters that represent environmental factors, and/or to model structure. Many, perhaps most, real-world perturbations of communities should be represented by changes to both variables and parameters. A severe flood, for instance, eradicates individual organisms and changes several environmental factors affecting populations. In the following, let P_v, P_p, and P_{vp} designate perturbations that change only variables, change only parameters, and those that change both, respectively.

Perturbations may cause other changes, such as alteration of the functional form of species interactions, that are not adequately represented by changes to variable or parameter values of typical community models, but which should be included in a comprehensive assessment of community's stability. Since these perturbations change community dynamics, they change *M*. How the altered community responds to these (and subsequent) perturbations must then be assessed against the new description of the community's dynamics as long as those dynamics remain altered. Although a completely adequate assessment of the ecological stability of a community requires consideration of all such changes caused by perturbations, most ecological modeling focuses on changes to variable and parameter values.

1.2. **Resistance, Resilience, Tolerance, and Ecological Stability**.

There are four plausible adequacy conditions for a definition of ecological stability:

(A1) the ecological stability of a biological community depends upon how it responds to perturbation ([A2]–[A4] specify the form of the required dependency);

(A2) of two communities *A* and *B*, the more ecologically stable community is the one that would exhibit less change if subject to a given perturbation *P*;

(A3) if *A* and *B* are in a pre-perturbation reference state or dynamic *R*, the more ecologically stable community is the one that would most rapidly return to *R* if subject to *P*; and,

(A4) if *A* and *B* are in *R*, the more ecologically stable community is the one that can withstand stronger perturbations and still return to *R*.

Before considering these conditions in detail, a few remarks help clarify their general basis. First, (A2)–(A4) only place *comparative* constraints on the concept of ecological stability and therefore require only a rank ordering of the stability of biological communities, rather than a particular quantitative valuation. The reason for requiring only comparative constraints is that quantitative valuation of ecological stability depend upon the system description (*M*) and reference state or dynamic (*R*) specified for a community, both of which may vary. Second, conditions (A2) and (A3) order the stability of communities based on their behavior following a *particular* perturbation *P*. As adequacy conditions, they therefore do not require a measure of the strength of perturbations. This reflects the difficulties facing the formulation of a measure of perturbation strength (see below), although such a measure is needed to evaluate the resistance of communities when only their responses to perturbations of different strength are known. If a quantitative measure of perturbation strength for different types of perturbation were available, two further *noncomparative* adequacy conditions could be formulated:

(A2′) a highly stable biological community should change little following weak perturbations; and,

(A3′) a highly stable biological community should rapidly return to its reference state or dynamic following weak perturbations.

In contrast, condition (A4) does require a measure of perturbation strength.

Condition (A1) captures the idea that a community's behavior is a reliable indicator of its ecological stability only if the behavior reflects how perturbation changes the community. If unperturbed, a community may exhibit great constancy throughout some period.[81] It may be, however, that if it had been even weakly perturbed, it would have changed dramatically. Constancy of this community surely does not indicate ecological stability when it would have changed substantially if perturbed slightly. Similarly, variability of a community does not necessarily indicate lack of ecological stability if it is the result of severe perturbations, perturbations that would cause greater fluctuations or even extinctions in less stable communities.

The reason for (A2) is that more stable communities should be less affected by perturbations than less stable ones. Communities that can withstand severe drought with little change, for instance, are intuitively more stable than those modified dramatically. This was the idea, for example, underlying MacArthur's (1955) definition of community stability (see Ch. 2, §2). The justification for (A3) is that more stable communities should more rapidly return to *R* following perturbations than less stable ones. This adequacy condition captures the idea that lake communities that return to *R* quickly after an incident of thermal pollution, for instance, are more stable than those with slower return rates following similar incidents. This idea was the implicit basis of the concept of

[81] As assessed by a lack of fluctuations in the biomasses of species in the community, for instance.

stability used by Rosenzweig and MacArthur (1963) to analyze predator-prey interactions (see Ch. 2, §3). The ground for the last condition is that communities that can sustain stronger perturbations than others and still return to R should be judged more stable. (A4) was the underlying basis, for instance, of Patten's (1961) measure of community stability (see Ch. 2, §3).

Three concepts – resistance, resilience, and tolerance – represent the properties required of ecological stability by (A2′)–(A4).[82] Resistance is inversely correlated with the degree a system changes relative to R following perturbation (P_v, P_p, or P_{vp}). Since perturbations vary in magnitude, resistance must be assessed against perturbation strength. Large changes after weak perturbations indicate low resistance; small changes after strong perturbations indicate high resistance. Resistance is thus inversely proportional to perturbation sensitivity.

Depending on M and R, changes in communities can be evaluated in different ways, each of which corresponds to a different measure of resistance. Community resistance is typically measured by changes in species *abundances* following perturbation. It could, however, be measured by changes in species *composition* following perturbation, or in some other way. Pimm's (1979) concept of species deletion stability, for instance, measures resistance by the number of subsequent extinctions in a community after one species is eradicated.

[82] The second part of this chapter (§2) argues ecological stability should not be defined as Lyapunov stability, local, global, or otherwise, and discusses structural stability.

A simple example illustrates the contextual import of *M* and *R* in assessing resistance. Consider the classical Lotka-Volterra model of a one-predator, one-prey community:

(2a) $$\frac{dx_y(t)}{dt} = ax_y(t) - \alpha x_y(t)x_d(t);$$

(2b) $$\frac{dx_d(t)}{dt} = -bx_d(t) + \beta x_d(t)x_y(t);$$

where x_d and x_y represent predator and prey populations; a represents prey birth rate; b represents predator death rate; and $\alpha, \beta > 0$ represent the effect of prey individuals on predator individuals and *vice versa*. Equation (2) is the description of the system, *M*. There is one nontrivial equilibrium, $x_d^* = \frac{b}{\beta}$ and $x_y^* = \frac{a}{\alpha}$, which is usually specified as the reference state, *R*.

For this *M* and *R*, resistance to a P_v perturbation that eradicates, say, half of x_y can be measured by how far x_d deviates from x_d^*, specifically, by $\frac{1}{\left|\max\{x_d(t)\} - x_d^*\right|}$ for $(\forall t > t_p)$ where t_p is the time of perturbation.[83] If *M* were different, the perturbation could obviously have a different effect on x_d. If x_d and x_y were competitors, for instance, x_d would increase rather than decrease after

[83] x_d decreases because x_y is its only food source according to (2). A more complete measure of resistance would also consider the subsequent deviation of x_y from x_y^* after being perturbed to half its initial value.

this perturbation. Similarly, if R were different, assessments of resistance may change. If R were the species composition x_d and x_y (*i.e.* $x_d, x_y > 0$) rather than their equilibrium values, for instance, resistance would be assessed in terms of changes from this composition, *i.e.* in terms of species extinction. The equilibrium $x_d^* = \frac{b}{\beta}$, $x_y^* = \frac{a}{\alpha}$ is globally stable for this simple community, so only a P_v perturbation strong enough to eradicate one of the species will cause extinction; this community returns to equilibrium after all other P_v perturbations. For communities with many species and more species dynamics, however, a P_v perturbation that eradicates half or less of one species may cause the extinction of that, or other species.

Different types of perturbations, moreover, yield different measures of resistance. Since evaluating resistance requires considering perturbation strength, strengths of different types of perturbations must be comparable for there to be a single measure of resistance for a system. Such comparisons are sometimes straightforward. If one perturbation eradicates half of species x in a community, for instance, another that eradicates 75% of x is certainly stronger. If another perturbation eradicates 25% of 3 species or 5% of 15 species in the community, however, it is unclear how its strength should be ranked against the perturbation that eradicates 75% of x. What criteria could be used to compare strengths of P_v, P_p, or P_{vp} perturbations, to which systems may show differential sensitivity, is

even less clear. Systems that are highly resistant to P_v perturbations may be extremely sensitive to even slight P_p. Comparing the resistance of communities is therefore only unproblematic with respect to perturbations of comparable kind.

Resilience is the rate at which a system returns to *R* following perturbation (P_v, P_p, or P_{vp}). Like resistance, resilience must be assessed against perturbation strength unless, although unlikely for many types of perturbation, return rate is independent of perturbation strength. Slow return rates after weak perturbations indicate low resilience and rapid rates following strong perturbations indicate high resilience.[84] Systems may not return to *R* after perturbation, especially following severe perturbation, so, unlike resistance, resilience is only assessable for perturbations that do not prevent return to *R*. Note that resilience and resistance are independent concepts: systems may be drastically changed by weak perturbations (low resistance) but rapidly return to *R* (high resilience), and *vice versa*.

Resilience is commonly measured as the inverse of the time taken for the effects of perturbation to decay relative to *R*. For a specific mathematical model, this can be determined analytically or by simulation. For the community described by equation (2) above, for instance, resilience to a P_v perturbation that eradicates half of one species could be simply measured by $\frac{1}{|t_{eq} - t_p|}$ where t_p is the time at

which the community is initially perturbed and t_{eq} is the time at which the community reestablishes equilibrium. Resilience to P_v perturbation is determined by the largest real eigenvalue part for systems modeled by linear differential equations if it is negative, and analytic methods have been developed to assess resilience to P_v perturbation for nonlinear models (see §2.3). Empirical measurement of resilience for communities in nature, however, is often thwarted by subsequent perturbations that disrupt return to *R*. This difficulty can be avoided if subsequent perturbations can be evaded with controlled experiments. If the return rate is independent of perturbation strength, estimation of resilience is also more feasible because only the decay rate of the perturbation effects need be measured before the system is further perturbed; measurement of perturbation strength is not required (Pimm 1984). Like resistance, furthermore, different types of perturbations yield different measures of resilience since return rate to *R* may depend upon the way in which systems are perturbed. A system may be highly resilient to P_v perturbation and poorly resistant to P_p perturbation, for instance, or more resilience to some P_v or P_p perturbations than others.

Tolerance, or "domain of attraction" stability, is the ability of a system to be perturbed and return to *R*, regardless of how much it may change and how long its return takes. More precisely, tolerance is positively correlated with the range

[84] If return rate does not depend on perturbation strength, however, resilience can be evaluated by the return rate independent of the perturbation strength, although the rate may vary across different types of perturbations.

and strength of perturbations a system can sustain and still return to R. The magnitudes of the strongest perturbations it can sustain determine the contours of this range. Note that tolerance is conceptually independent of resistance and resilience: a system may be severely perturbed and still return to R (high tolerance), even if it changes considerably (low resistance) and its return rate is slow (low resilience), and *vice versa*.

Similar to resistance and resilience, different kinds of perturbations yield different measures of tolerance. Tolerance to P_v perturbations, for instance, is determined by the maximal changes variables can bear and not jeopardize the system's return to R. With respect to P_v perturbations that affect only one species of a community, for instance, tolerance can be simply measured by the proportion of that species that can be eradicated without precluding the community's return to R. If a nontrivial equilibrium of equation (2) from above is globally stable, for instance, the community described by the equation is maximally tolerant to P_v perturbations relative to this reference state because the community will return to it after any P_v perturbation that does not eradicate one of the species. Variables of a system may be perturbed, however, in other ways. A P_v perturbation may change all variables, several, or only one; it may change them to the same degree, some variables more severely than others; and so on. How exactly variables are perturbed may affect whether the system returns to R. System tolerance must therefore be evaluated with respect to different types of perturbation. The same

goes for assessing tolerance to P_p or P_{vp} perturbations. Note that local asymptotic Lyapunov stability corresponds to tolerance to P_v perturbation in the infinitesimal neighborhood of an equilibrium, and global asymptotic Lyapunov stability corresponds to tolerance to any P_v perturbation (see §2).

Although resistance, resilience, and tolerance do not adequately explicate ecological stability individually, they do so collectively. In fact, they constitute jointly sufficient and separately necessary conditions for ecological stability, notwithstanding Shrader-Freschette and McCoy's (1993, 58) claim that such conditions do not exist. Consider sufficiency first. Since these three concepts represent the properties underlying conditions (A2)–(A4) [and (A2′) and (A3′)], communities exhibiting them to a high degree would change little after strong perturbations ([A2]), return to *R* rapidly if perturbed from it ([A3]), and return to *R* following almost any perturbation ([A4]).[85] As such, these three properties certainly capture ecologists' early conceptions of ecological stability (see Ch. 2), and there seems to be no further requirement of ecological stability that a community exhibiting these properties would lack.

Each concept is also necessary. Highly tolerant and resistant communities, for instance, change little and return to *R* after most perturbations. In regularly perturbing environments, however, even a highly resistant and tolerant

[85] If *R* is a point equilibrium, moreover, a community exhibiting high resistance, resilience and tolerance will be relatively constant.

community may be iteratively perturbed to the boundary of its tolerance range and "linger" there if its return rate to *R* is too slow. Subsequent perturbations may then displace it from this range, thereby precluding return to *R*. If this community rapidly returned to *R* after most perturbations (high resilience), it would rarely reach and would not linger at its tolerance boundary. In general, low resilience preserves the effects perturbations have on communities for extended, perhaps indefinite durations, which seems incompatible with ecological stability.

Similar considerations show tolerance and resistance are necessary for ecological stability. A highly resilient and tolerant but weakly resistant community rapidly returns to *R* following almost any perturbation, but changes significantly after even the slightest perturbation, which seems contrary to ecological stability. The dramatic fluctuation such communities would exhibit in negligibly variable environments is the basis for according them low ecological stability. A highly resilient and resistant but weakly tolerant community changes little and rapidly returns to *R* when perturbed within its tolerance range, but even weak perturbations displace it from this range and thereby preclude its return to *R*, which also seems contrary to ecological stability.

Resistance, resilience, and tolerance are independent concepts and thus biological communities may exhibit them to different degrees. Alhough the necessity of each concept for ecological stability does not strictly entail they are equally important in evaluations of a community's stability, nothing about the

pre-theoretic concept of ecological stability seems to suggest otherwise. As a concept composed of resistance, resilience, and tolerance, ecological stability therefore imposes only a partial, not complete, ordering on communities. Moreover, since communities may differentially exhibit resistance, resilience, and/or tolerance for different types of ecological perturbations (see §1.1), each property also imposes only a partial ordering on communities. This twofold partiality entails inferences from analyses of stability-diversity and stability-complexity relationships are limited by the property and type of perturbations analyzed, beside the particular system description (*M*) and reference state or dynamic (*R*) specified.

1.3. Constancy and Ecological Stability.

Compared with resistance, resilience, and tolerance, constancy is a fundamentally different kind of concept. Unlike them, it is not defined in terms of response to perturbation, and thus violates adequacy condition (A1), as well as (A2)–(A4). Rather, constancy of a biological community is typically defined as a function of the variances and/or covariances in species biomasses.[86] Tilman (1996, 1999; Lehman and Tilman 2000), for instance, defined ecological stability as "temporal stability" (S_t):

[86] If *R* refers to a specific set of species, constancy can also be measured by the variability of the species composition of a community.

$$(3) \qquad S_t(C) = \frac{\sum_{i=1}^{n} \overline{B_i}}{\sqrt{\sum_{i=1}^{n} Var(B_i) + \sum_{\substack{i=1;\, j=1 \\ i \neq j}}^{n} Cov(B_i, B_j)}};$$

where C designates an n-species communities; B_i is a random variable designating the biomass of species i in an n-species community C assayed during some time period, and let $\overline{B_i}$ designate the expected value of B_i for the time period it is assayed; *Var* designates variance; and *Cov* designates covariance. The motivating intuition for this definition is the idea that if two series of abundances are plotted across time, the more stable one exhibits less fluctuation (Lehman and Tilman 2000). In particular, if a community becomes more variable as judged by variances and covariances between its biomasses, regardless of what causes the variability, the denominator of (3) increases and its temporal stability decreases. One counterintuitive feature of this definition is that a community could become more stable solely because mean biomasses increase.[87] This problem is easily avoided by measuring constancy strictly in terms of biomass variability [*e.g.* reformulating (3) with a numerator of 1], but this does not circumvent the fundamental difficulty that defining ecological stability as constancy does not satisfy (A1), irrespective of how constancy is measured. Contrary to the intuition motivating this definition, however, constancy is neither necessary nor sufficient

[87] Tilman's definition also initiated a controversy about whether it biases the stability-diversity debate in the positive See Doak *et al*. 1998, Tilman *et al*. 1998, and Chapter 6.

for ecological stability. It is insufficient because a community may exhibit great constancy if unperturbed, but change dramatically if it were even weakly perturbed.[88] Unless constancy is a result of how a community responds to perturbation, it can mask extreme sensitivity to perturbation, which is incompatible with ecological stability. By itself, therefore, constancy is not a reliable indicator of ecological stability.

Constancy is not necessary for ecological stability for two reasons. First, although a highly stable community at equilibrium remains relatively constant, it may fluctuate if subject to severe perturbations, perturbations that would drastically modify or eradicate weakly stable communities. It would be unjustifiable to regard these fluctuations as evidence of low ecological stability. The problem is that because constancy is not defined relative to perturbation response, it cannot distinguish between fluctuations that are a consequence of strong perturbation, which are consistent with ecological stability, and those that reveal susceptibility to weak or moderate perturbations, which are incompatible with ecological stability.

The second reason constancy is not necessary is that a highly stable system will not be constant if R is not an equilibrium reference state. Communities may be highly resistant, resilient, and tolerant with respect to

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[88] The extreme case is that a system at a Lyapunov *unstable* equilibrium remains constant if unperturbed.

regular limit cycles or more complicated attractor dynamics. In this case, the community changes little relative to the limit cycle or attractor after strong perturbation, rapidly returns to the limit cycle or attractor after strong perturbation, and returns to the limit cycle or attractor even after severe perturbation. Lack of constancy of such a community does not detract from the fact that any adequate conception of ecological stability should judge it highly stable relative to *R*.[89]

Most classifications of ecological stability include an additional non-perturbation based stability concept, persistence: the time a community remains in *R* irrespective of whether or not it is perturbed. Retaining a particular species composition or biomasses within delimited ranges are typical reference states for gauging persistence. Persistence is usually measured by how long they do or are predicted to exhibit these states. It could, for instance, be measured by the time minimum population levels have been sustained (*e.g.* non-zero levels), or will be sustained based on predictions from mathematical models (Orians 1975). As such, persistence is in fact only a special case of constancy in which constancy is measured by the time *R* has been or will be exhibited, rather than variability with respect to *R*. Understood as the absence of species extinction, persistence is

[89] This problem can be avoided by relativizing constancy to *R*. In this case, constancy would be equivalent to variability *from R*. This relativization does not circumvent the first problem discussed above, however.

certainly a necessary condition for ecological stability, but certainly not constitutive of it.

Table 1 presents a taxonomy of the stability concepts: resistance, resilience, tolerance, constancy, local and global Lyapunov stability, and structural stability. The taxonomy classifies these concepts into two general categories, defines each, and lists some of their properties.

This taxonomy subsumes other classifications in the ecological literature. Lewontin's (1969) was the first and included local and global Lyapunov stability, structural stability, constancy, and, though not by these labels, resilience and tolerance to P_v perturbations (see Ch. 2). Orians' (1975) was the second. He left Lyapunov and structural stability out of his classification, but included constancy, resistance under the label 'inertia,' resilience under the label 'elasticity,' tolerance under the label 'amplitude,' as well as persistence as a distinct stability concept. Orians' classification also included two additional concepts that have counterparts in the above framework. The first, 'cyclic stability,' is equivalent to resistance, resilience, and tolerance relative to a limit cycle reference state. Orians intended the second, 'trajectory stability,' to capture the idea of the stability of community succession. It is equivalent to tolerance with R specified as the hypothesized climax community.

Pimm (1984) presented the same classification as Lewontin (1969) except resistance was included and structural stability was not. Pimm (1984) also first

recognized that attributions of ecological stability must be made with respect to a "variable of interest." The system description (*M*) specifies the variables that represent the system in our framework. Pimm did not, however, relativize ecological stability to an explicit reference state or dynamic. Grimm and Wissel (1997) were probably the first to make this contextualization explicit, thereby allowing communities exhibiting limit cycles or strange attractor dynamics to be judged ecologically stable. They resolved ecological stability into six concepts: constancy, persistence, resistance, resilience under the label 'elasticity', tolerance under the label 'domain of attraction', and a concept representing that the system returns to *R* after perturbation under the label 'resilience'. Whether a system returns to *R* after perturbation depends upon the type and strength of the perturbation and the system's tolerance, so the last of Grimm and Wissel's stability concepts ('resilience') seems to be a special case of tolerance.

1.4. **The Conceptual Status of Ecological Stability**.

It is worth pausing over what the framework for ecological stability presented above shows about the general concept. It certainly shows that ecologists have used the term 'stability' to describe several distinct features of community dynamics, although only resistance, resilience, and tolerance adequately define ecological stability. This plurality does not manifest, however, an underlying vagueness, "conceptual incoherence," or "inconsistency" of the

concept, as Shrader-Frechette and McCoy (1993, 57) suggest in their general critique of basic ecological concepts and ecological theories based on them.

Two claims seem to ground their criticism. First, if 'stability' is used to designate distinct properties, as it has been in the ecological literature (see Ch. 2), this indicates the concept is itself conceptually vague and thereby flawed. Although terminological ambiguity is certainly undesirable, most ecologists unambiguously used the term to refer to a specific property of a community and accompanied the term with a precise mathematical or empirical operationalization (see §§2–4). Since these were in no sense vague, in no sense was ecological stability "vaguely defined" (Shrader-Frechette and McCoy 1993, 40). Ecologists quickly appreciated this terminological ambiguity, moreover, and began explicitly distinguishing different senses of ecological stability with different terms (Odenbaugh 2001). Lewontin's (1969) review was the first example, and subsequent analyses of the concept did not abandon this insight.

Shrader-Frechette and McCoy's second claim is that, "There is no homogeneous class of processes or relationships that exhibit stability," (1993, 58). The underlying assumption seems to be that concepts in general, ecological stability in particular, must refer to a homogeneous class to be conceptually unproblematic. That ecological stability does not, and worse, that ecologists have supposedly attributed inconsistent meanings to it, shows the concept is incoherent, they believe, much like the vexed species concept (1993, 57).

Shrader-Frechette and McCoy do not offer an argument for this assumption, and it is indefensible as a general claim about what concepts must refer to. Common concepts provide clear counterexamples. The concepts 'sibling,' 'crystal,' and 'field,' for instance, refer to heterogeneous classes, but there is nothing conceptually problematic about them. There is debate about the idea of disjunctive *properties* in work on multiple realization (Fodor 1974; Kim 1998; Batterman 2000), but criticisms raised against disjunctive properties do not necessarily apply to disjunctive *concepts*, nor were they intended to. Kim (1999, 110) emphasizes this point:

> Qua property, dormativity is heterogeneous and disjunctive, and it lacks the kind of causal homogeneity and projectability that we demand from kinds and properties useful in formulating laws and explanations. But [the concept of] dormativity may well serve important conceptual and epistemic needs, by grouping properties that share features of interest to us in a given context of inquiry.

Even if criticisms of disjunctive properties were sound, it therefore would not follow that the disjunctive concepts such as ecological stability are also problematic.[90] Shrader-Frechette and McCoy's criticism of ecological stability is therefore indefensible. The conceptual and epistemic utility of a concept is enhanced, furthermore, if clear guidelines for its application exist, which Sections 1.2 and 1.3 have attempted to describe.

Moreover, the definitional status of the concepts of ecological stability and species is not analogous. Biologists have proposed plausible, but incompatible

[90] No assumption about whether ecological stability is or is not a property is being made.

competing definitions for the species concept because it is problematically ambiguous (Ereshefsky 2001). That resistance, resilience, and tolerance have been referred to under the rubric 'stability,' however, do not show ecological stability is similarly problematically ambiguous because they are conceptually independent and therefore compatible, as different senses of 'species' are not.[91] In addition, as classifications of different stability concepts attest (*e.g.* Lewontin 1969; Orians 1975; Pimm 1984), most ecologists recognized that there are several components of ecological stability, and individual stability concepts such as resistance, resilience and tolerance, or measures thereof, were rarely proposed as *the* uniquely correct definition of ecological stability. Rather, they were and should be understood as distinct features of ecological stability or ways of measuring it, not competing definitional candidates. Like many scientific concepts, ecological stability is multifaceted, and the distinct referents ecologists attributed to it accurately reflect this. Conceptual multifacetedness alone does not entail conceptual incoherence or inconsistency.

2. Ecological and Lyapunov Stability.

2.1. Introduction.

[91] As noted above, different quantitative *measures* of resistance, resilience, and tolerance may be incompatible. This does not establish, however, that the corresponding *concepts* are incompatible.

The first part of this chapter presented a comprehensive classification of different features of ecological stability and argued that resistance, resilience, and tolerance collectively define the concept of ecological stability adequately while constancy is neither necessary nor sufficient for it. The second part of the chapter shows why ecological stability should not be defined as Lyapunov stability, as is commonly assumed in mathematical modeling of biological communities.

Lyapunov stability is named after the Russian mathematician who first precisely defined the concept to describe the apparently stable equilibrium behavior of the solar system (Lyapunov 1892). His definition has found widespread application outside this context and is frequently used to analyze mathematical models of biological communities (Logofet 1993). Robert May (1974) used this definition, for instance, in his influential analysis of the relationship between the stability and complexity of such models (see Ch. 1, §4).

The definition has some clear advantages. Unlike other definitions, it integrates ecological stability into a thoroughly studied mathematical theory that has proved fruitful in the analysis of mechanics, electrical circuits, economic systems, and other systems in applied mathematics. It also seems to formalize the intuition that ecological stability depends on community response to perturbation. Despite these apparent advantages, ecological stability should not be defined as Lyapunov stability.

Sections 2.3 and 2.3 describe the concept of Lyapunov stability, its underlying mathematical theory, and show why this theory is so successful within physics. Section 2.4 considers the apparent advantages of the definition and illustrates how Lyapunov stability applies to mathematical models of biological communities. Section 2.5 argues this definition is problematic, focusing specifically on biological interpretation of Lyapunov stability. Based on this analysis, Section 2.6 draws some general conclusions about scientific definition and illustrates an important limitation of the theory of Lyapunov stability within mathematical ecology.

2.2. **Lyapunov Stability**.

To ensure sufficient generality, represent a system by a position vector $\mathbf{x}(t)$ (t represents time) in an abstract n-dimensional state space E. Assume E is governed by a vector function $\mathbf{F}$ representing the magnitude and change of direction it induces on $\mathbf{x}(t)$. $\mathbf{F}$ represents, therefore, the dynamics of the system $\mathbf{x}(t)$. Points in E for which $\mathbf{F}=0$ are called equilibrium points, and unperturbed position vectors at such points remain stationary.

Lyapunov stability is a property of system behavior in neighborhoods of equilibria. Specifically, an equilibrium $\mathbf{x}^*$ is *Lyapunov stable* in E_x ($\mathbf{x}^* \in E_x \subseteq E$) iff:

(4) $$(\forall \varepsilon > 0)(\exists \delta > 0)(|\mathbf{x}(t_0) - \mathbf{x}^*| < \delta \Rightarrow (\forall t \geq t_0)(|\mathbf{x}(t) - \mathbf{x}^*| < \varepsilon));$$

where ε and δ are real values, $\mathbf{x}(t_0) \in E_x$ represents the system at some initial time t_0, and '$|\cdot|$' designates a distance metric on E. Informally, (4) says $\mathbf{x}^*$ is Lyapunov stable if systems beginning in $\mathbf{x}^*$ neighborhoods remain near it after perturbations that do not displace them from E_x. $\mathbf{x}^*$ is *asymptotically Lyapunov stable* in E_x iff (4) and $\lim_{t\to\infty} \mathbf{x}(t) = \mathbf{x}^*$. The subspace E_x of E within which systems are (asymptotically) Lyapunov stable is called the (*attraction*) *stability domain* of $\mathbf{x}^*$ (see Figure 2). If the (attraction) stability domain of $\mathbf{x}^*$ is all of E, $\mathbf{x}^*$ is (asymptotically and) globally Lyapunov stable.

In general, Lyapunov stability cannot be assessed with (4) because explicit solutions for $\mathbf{x}(t)$ can seldom be found. Scientific models often characterize $\mathbf{x}(t)$ in terms of differential equations:

$$(5) \qquad \frac{d\mathbf{x}(t)}{dt} = \mathbf{F}(\mathbf{x}(t), \Omega);$$

where Ω is a set of parameters designating factors that influence system dynamics but are uninfluenced by them, and $\mathbf{F}$ is a $n \times n$ matrix $[a_{ij}]$.[92] For the complex systems modeled by equation (5) that scientists study, explicit solutions for $\mathbf{x}(t)$ are rarely available. Without such solutions, system behavior as required by (4) cannot be directly evaluated.

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[92] Since $\mathbf{F}$ is not a function of t, (5) represents *autonomous* dynamic systems that do not explicitly depend on time. These models are common in science and the focus of the following analysis.

2.3. **The Direct and Indirect Methods**.

Lyapunov (1892) recognized this difficulty and developed two methods for assessing (4) indirectly. The first 'indirect method' involves linearizing **F** at $\mathbf{x}^*$. Specifically, let $\mathbf{A} = \left.\frac{\partial \mathbf{F}(\mathbf{x}(t),\Omega)}{\partial \mathbf{x}}\right|_{\mathbf{x}=\mathbf{x}^*}$ be the Jacobian matrix of **F** evaluated at $\mathbf{x}^*$. The eigenvalues of **A** determine whether $\mathbf{x}^*$ is stable. These are scalar values λ_i such that $\det(\mathbf{A}-\lambda_i\mathbf{I})=0$, *i.e*. the roots of the characteristic polynomial of **A**. Lyapunov proved $\mathbf{x}^*$ is asymptotically Lyapunov stable iff:

(6) $\mathrm{Re}\lambda_i(\mathbf{A})<0$ for $i=1,\ldots,n$;

where $\mathrm{Re}\lambda_i(\mathbf{A})$ designates the real part of the *i*th eigenvalue of **A**, λ_i. Since **A** is only defined at $\mathbf{x}^*$, stability determined by the indirect method is restricted to infinitesimal neighborhoods of $\mathbf{x}^*$. For this reason, it is called *local stability*. The indirect method is prevalent in mathematical modeling because it is almost universally applicable: it applies to any system representable by differential equations like (5) and some difference equations (Hinrichsen and Pritchard 2005).

Stability criteria based on the indirect method such as (4) have a serious limitation: they provide no information about the extent of (attraction) stability domains. This prompted Lyapunov (1892) to develop a "direct method" for evaluating (4). It involves constructing a differentiable scalar Lyapunov function $V(\mathbf{x})$ with an origin at $\mathbf{x}^*$ (*i.e*. $\mathbf{x}^*=\mathbf{0}$) such that:

(i) $V(\mathbf{x})$ is positive definite: (a) $V(\mathbf{0})=0$; (b) $V(\mathbf{x})>0$ for all $\mathbf{x}\neq\mathbf{0}$; and,

(ii) $\nabla V(\mathbf{x})\cdot\mathbf{F}(\mathbf{x},\Omega)\leq 0$ for all $\mathbf{x}$;

where '$\cdot$' designates the dot product, and '∇' designates the gradient vector function. Lyapunov (1892) proved the existence of a Lyapunov function on $E_x \subseteq E$ ($\mathbf{x}^* \in E_x$) is sufficient for Lyapunov stability of $\mathbf{x}^*$ in this region, and with strict inequality in (ii), $\mathbf{x}^*$ is asymptotically Lyapunov stable. This condition was also later proved necessary (Hahn 1963). Thus, the ability to construct Lyapunov functions is a stability criterion. As a methodology, it is labeled direct because its success depends directly upon the mathematical form of equations like (5), unlike the indirect method, which relies on their linearization, and unlike direct evaluation of (4), which requires explicit solutions to (5).

Although no general method for constructing Lyapunov functions is known, the direct method has proven to be an extremely useful tool for analyzing physical systems, especially in the classical framework governed by only Newtonian mechanics and friction. Across scientific fields, this is the exception rather than the rule. Constructing Lyapunov functions is difficult if not impossible for the predominantly nonlinear systems scientists study (Goh 1977). The reason for its utility in the classical framework is twofold. First, there are highly confirmed mathematical models describing numerous kinds of systems in this framework. The likelihood is therefore high that application of the direct method to these models will reveal the true stability properties of the systems they represent. Second, in the classical framework certain quantities, such as total

energy, are conserved or monotonically dissipated in such systems, depending on whether they are characterized as open or closed. These quantities ensure Lyapunov functions exist for models of these systems. Lyapunov, in fact, developed the Lyapunov function to generalize the classical energy concept and his proof about its connection to stability depends essentially on energy conservation (Lyapunov [1892] 1992).

To illustrate, consider a closed particle mass system governed by a conservative force field **G** in a frictionless Newtonian framework. The system energy, $V(\mathbf{x},\mathbf{v})$, is:

(7) $V(\mathbf{x},\mathbf{v})=\frac{1}{2}m|\boldsymbol{v}|^2+U(\mathbf{x})$;

where **x** is a position vector, **v** is a velocity vector, m represents particle mass, '$|\cdot|$' designates the magnitude of $\cdot$, and U is a scalar potential energy function such that $\mathbf{G}(\mathbf{x})=-\nabla U(\mathbf{x})$.[93] Energy conservation ensures:

(8) $V(\mathbf{x},\mathbf{v})=c$;

where c is a constant real value. At an equilibrium $\mathbf{x}^*$, $\mathbf{v}=\mathbf{0}$, $\mathbf{G}=\mathbf{0}$ and hence $\text{grad}U(\mathbf{x})=\mathbf{0}$. If, furthermore, $\mathbf{x}^*$ is a local minimum of $U(\mathbf{x})$, an "energy difference" function $V^*(\mathbf{x},\mathbf{v})$ can be defined such that $V^*(\mathbf{x},\mathbf{v})=V(\mathbf{x},\mathbf{v})-V(\mathbf{x}^*,\mathbf{0})$. $V^*(\mathbf{x},\mathbf{v})$ is a Lyapunov function and, therefore, $\mathbf{x}^*$ is stable. In this case, energy conservation entails (ii) from above is satisfied by equality. If, however, energy

[93] Note that $V(\mathbf{x},\mathbf{v})$ is the Hamiltonian of this system.

were continually decreasing instead of conserved, by friction for instance, (ii) would be satisfied by strict inequality and $\mathbf{x}^*$ would be asymptotically stable.

Within the classical framework, stability properties of models of more complicated systems that include and disregard friction can be evaluated with the direct method. The method is also useful in non-classical frameworks with similar properties, such as mass-energy conservation in special relativity theory. The equations characterizing systems in these and the classical framework are often too complex to solve analytically, and the direct method provides the only means by which the attraction domains of asymptotically stable equilibria can be determined. In a wide variety of frameworks within physics, therefore, the direct method and the concept of Lyapunov stability are indispensable.

2.4. Lyapunov Theory and Community Modeling.

The brief outline of Lyapunov theory above suggests some important advantages of defining ecological stability as Lyapunov stability. First, the definition formalizes the concept and integrates it into a well-developed mathematical theory. Stability properties of mathematical models of communities can then be assessed with thoroughly studied analytical techniques.

Besides the virtues of formalization, Lyapunov stability also seems to capture precisely the intuition that ecological stability depends upon community response to perturbation. Consulting (4), think of a community perturbed at time

t_0 from $\mathbf{x}^*$ to $\mathbf{x}(t_0)$ such that $|\mathbf{x}(t_0)-\mathbf{x}^*|<\delta$. If $\mathbf{x}^*$ is Lyapunov stable, (4) states that the perturbed community will remain in an ε-neighborhood of $\mathbf{x}^*$ for $\forall t \geq t_0$, *i.e.* the effects of the perturbation are circumscribed. Some other popular definitions of ecological stability are mathematically precise in that they are statistical functions of model variables (*e.g.* Lehman and Tilman's [2000] 'temporal stability'), but they do not, as Lyapunov stability does, provide a mathematical characterization of equilibrium system dynamics. If $\mathbf{x}^*$ is Lyapunov stable in some region of the state space *E*, for instance, the conditional in (4) ensures predictions can be made about system behavior after perturbation from $\mathbf{x}^*$. Mathematical definitions in the statistical sense cannot ground such predictions unless future values of variables depend upon past values in some systematic way, and the precise form of the dependency is known. The concept of Lyapunov stability is an important analytic tool within physics because (1) provides a mathematically precise description of the equilibrium dynamics of systems.

In addition, properties of community response to perturbation that are fundamental components of ecological stability *seem* to be formalizable with the direct method. The size of attraction domains of asymptotically Lyapunov stable equilibria and the rate systems return to them, for instance, are definable in terms of Lyapunov functions (Hahn 1963, §§12, 22-25). The larger the attraction domain, for instance, the stronger the perturbations of variables a system can sustain and return to $\mathbf{x}^*$, which is often called system 'tolerance'. Similarly, the

"steeper" the Lyapunov function $V(\mathbf{x})$ (as gauged by $\nabla V(\mathbf{x})$), the faster it returns to $\mathbf{x}^*$, often called system 'resilience'. If Lyapunov stability adequately defined ecological stability, it would therefore be possible to formalize the properties of tolerance and resilience and their relation to the stability of biological communities. Specifically, the intuitive ideas that ecological stability increases with the strength of perturbation from which a system can return to equilibrium (see [A4], §1.2), and with the speed of return to equilibrium after perturbation (see [A3], §1.2), would be formalizable.

Finally, the direct method adequately characterizes the equilibrium dynamics of many systems studied in physics (and other sciences), and it is reasonable to expect the method will fare similarly for ecological systems since their models share a similar mathematical structure. Like systems studied in physics, biological communities are usually modeled by differential equations. The only difference is that components of the vector $\mathbf{x}(t)=\langle x_1(t),\ldots,x_i(t),\ldots,x_n(t)\rangle$ represent biological variables, usually population sizes of species in a community, instead of typical physical variables.

This expectation seems to be supported, for instance, by the classical Lotka-Volterra model of one-predator, one-prey communities:

(9a) $$\frac{dx_y(t)}{dt} = ax_y(t) - \alpha x_y(t)x_d(t);$$

(9b) $$\frac{dx_d(t)}{dt} = -bx_d(t) + \beta x_d(t)x_y(t);$$

where x_d and x_y represent predator and prey population sizes; a represents prey birth rate; b represents predator death rate; and $\alpha,\beta>0$ represent the effect of prey individuals on predator individuals and *vice versa*. Setting $\frac{dx_y(t)}{dt}$ and $\frac{dx_d(t)}{dt}$ to 0 and solving for x_d and x_y yields one nontrivial equilibrium $\mathbf{x}^*$ where $x_d^* = \frac{b}{\beta}$ and $x_y^* = \frac{a}{\alpha}$. A Lyapunov function exists for all $x_d, x_y > 0$:

(10) $$V(\mathbf{x}) = c_1(x_y - x_y^* \ln x_y) + c_2(x_d - x_d^* \ln x_d);$$

where $c_1, c_2 > 0$ are constants, so $\mathbf{x}^*$ is globally stable by the direct method (Logofet 1993).

An interesting property of equation (9) discovered by Vito Volterra reveals a structural similarity between models of ecological and physical systems, which in turn seems to justify the utility of Lyapunov theory in ecology. Equation (9) can be rewritten as:

(11a) $$\gamma_1 \dot{x}_y = \gamma_1 a x_y(t) - x_y(t) x_d(t);$$

(11b) $$\gamma_2 \dot{x}_d = -\gamma_2 b x_d(t) + x_d(t) x_y(t);$$

where $\dot{x}_y = \frac{dx_y(t)}{dt}$, $\dot{x}_d = \frac{dx_d(t)}{dt}$, $\gamma_1 = \frac{1}{\alpha}$, and $\gamma_2 = \frac{1}{\beta}$. Adding these equations and integrating yields:

$$(12) \qquad \gamma_1 \dot{x}_y + \gamma_2 \dot{x}_d + \gamma_1 a \int_0^t x_y(t) - \gamma_2 b \int_0^t x_d(t) = c,$$

where c is a constant real value. Volterra believed (9) corresponded to a form of energy conservation [compare with (4) and (5) above].[94] He called the first two terms "actual demographic energy," and the second two "potential demographic energy" (Scudo 1971).[95] If this structural similarity generalizes broadly across mathematical models of ecological systems, a view shared by another prominent founder of mathematical ecology Alfred Lotka (1956), it would seem to indicate that the stability definition used in physics is appropriate for ecology.

2.5. **Lyapunov Stability in an Ecological Context**.

The adequacy of a definition depends upon what it requires of the defined concept. If ecological stability is defined as Lyapunov stability, for instance, the latter stipulates conditions biological communities must satisfy to be ecologically stable. If these conditions are unreasonable – if they are biologically unrealistic, too weak, or too strong for instance – the definition is inadequate. Such a definition would violate the similarity or fruitfulness criteria, or both. Despite its apparent advantages, interpreting Lyapunov stability in ecological terms furnishes strong reasons for rejecting the definition.

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[94] (12), in fact, is the underlying basis of (10). See Logofet (1993, 111-114).

[95] At least for the first two terms, the resemblance with energy conservation is somewhat weak. The "actual demographic energy" corresponds closely with the mathematical form for the momentum of two particles, not their kinetic energy.

There are four types of Lyapunov stability to consider as definitional candidates for ecological stability. In order of increasing strength, they are local Lyapunov stability, nonasymptotic stability within a nontrivial stability domain, asymptotic stability within a nontrivial domain, and global asymptotic stability. Consider the weakest form first. Although the frequent focus of community modeling, perhaps because it is relatively easy to evaluate with the indirect method (Hastings 1988), local stability clearly defines ecological stability poorly. Differentiable models of systems can be linearized with the Jacobian matrix at any point of state space, such as at an equilibrium (see §2.3). By itself, however, linearization only provides information about local system behavior, *i.e*. only in an *infinitesimal* neighborhood of the linearization point. Local stability therefore says nothing about system behavior outside this extremely restricted domain. Besides it being fundamentally unclear how perturbation within an infinitesimal domain can be biologically interpreted (or empirically measured), real-world perturbations are clearly not of infinitesimal magnitude. Any real perturbation will expel a system at a strictly locally stable equilibrium from its stability domain. Local stability of nonlinear systems like biological communities consequently provides no information about their response to common perturbations like drought, fire, population reduction by disease, *etc*. Application of the indirect method to mathematical models of communities, which can only

evaluate local stability, therefore yields negligible insight into the dynamics of biological communities relevant to ecological stability.[96]

For different reasons, Mikkelson (1997) reaches a similar conclusion about local stability. His argument is based on the principle: "Do not employ a definition that turns what was originally thought to be an important empirical matter into a generic a priori exercise" (1997, 483). Applying this principle to the task of defining ecological stability, Mikkelson continues (1997, 485):

> Requiring that every single species in a fifty-species community have a given property –*any* property– is a much stricter criterion than requiring that every species in a ten-species community have the same property. This means that as the number of species increases, the probability that the criteria are met almost certainly decreases. This leads to a *default* expectation that stability will decline with increasing diversity.

Since local stability requires *every* species return to its preperturbation value, Mikkelson claims that defining ecological stability as local stability decreases the likelihood species rich communities will be stable. It thereby biases *a priori* the debate about the relationship between community stability and diversity (construed as species richness) towards an inverse relationship, and violates his principle. On this basis, Mikkelson concludes the definition is indefensible.

The first problem with this argument is Mikkelson's assumption (the "default expectation") that the likelihood of local stability of communities generally decreases with increasing species richness (1997, 494). This assumption

[96] Food web modeling of community stability is based on the indirect method, and has been criticized for this reason (Hastings 1988).

is the underlying basis of the long quote above, but its truth is, however, an empirical rather than *a priori* issue. Interspecific interactions that emerge with greater species richness often increase the likelihood of stability, as the stabilizing effect of adding species to some community models shows (May 1974).

The second problem is that Mikkelson's principle is an unjustifiable adequacy condition for definitions in science because it confers too much import to unresolved scientific questions, regardless of how poorly formulated they may be. According to the principle, scientific concepts should not be defined in ways that resolve, even partially, outstanding questions that involve them. Yet scientific questions may themselves be ill-formed or confused due to ambiguity or vagueness of the concepts they concern. In fact, Shrader-Frechette and McCoy (1993) argue the stability-diversity-complexity debate of community ecology is itself such an example. Although it would plainly be indefensible for a definition to stipulate a resolution of a conceptually unproblematic, clearly empirical scientific question, apparently intractable scientific debates and recalcitrant questions are sometimes justifiably resolved or, more accurately, dissolved when precise definitions of concepts reveal their misguided nature.[97]

The stronger concept of nonasymptotic Lyapunov stability within a nonlocal domain also inadequately defines ecological stability. Without

[97] Einstein's definition of simultaneity, for instance, arguably settled a number of scientific questions about temporal relations between events. Thanks to Mark Colyvan for bringing this example to my attention.

asymptotic dynamics driving systems perturbed from equilibrium to return to it, successive weak perturbations can displace communities from their stability domains and, in the extreme case, cause species eradication. Ecological stability undeniably requires, however, persistence of the species of a community subject to successive weak perturbations.

Even with asymptotic dynamics, however, Lyapunov stability does not define ecological stability adequately. To see why, consider defining ecological stability as the strongest Lyapunov stability property: global asymptotic stability. Unlike the Lyapunov stability properties considered thus far, global asymptotic stability appears to be much stronger than ecological stability because it seems to entail that a community will return to equilibrium following any perturbation that does not eradicate its species. Model variables of systems at asymptotically and globally stable equilibria that are perturbed to 1% of their equilibrium values, for instance, will deterministically return to their initial values.[98] This response to such severe perturbations is not required for a biological community to be ecologically stable, but it certainly seems sufficient.

Despite its apparent plausibility, the idea that global asymptotic Lyapunov stability is sufficient (but not necessary) for ecological stability is unjustified. It is based on a flawed conception of ecological perturbation. Real-world perturbations

[98] If the model includes stochastic processes, they may further propel variables to zero. The possibility of such a chance occurrence, however, does not detract from the underlying stability of this system's dynamics.

to biological communities do not merely affect the population sizes of their species, represented by variables in models like (5). They also change environmental factors that influence community dynamics, represented by model parameters, as well as affect community structure, represented by model structure. As May (1974, 216) creatively put it:

> in nature, population perturbations are driven not by the stroke of a mathematician's pen resetting initial conditions [*i.e*. resetting variable values to represent perturbations], but by fluctuations and changes in environmental parameters such as birth rates, carrying capacities, and so on.

Perturbations may induce, for instance, changes in the strength and qualitative nature of interspecific and intraspecific community interactions. Initially noninteracting species may begin competing or exhibiting other non-neutral interactions, and *vice versa*. Since real-world perturbations may affect environmental factors that influence community dynamics as well as population sizes of species, they should be represented by corresponding changes in variable *and* parameter values. Ecological stability should then be evaluated with respect to system behavior following both types of changes.

Lyapunov stability, however, only assesses system response to temporary changes in variable values (P_v perturbations; see [4] above). It does not consider system responses to changes in parameters (P_p perturbations) and thus provides only a partial account of the type of system response to perturbation ecological stability requires. Lyapunov's direct method is therefore not a suitable

methodology for analyzing ecologically relevant nonlocal stability properties of standard community models, although it accurately estimates stability to P_v perturbations that affect only model variables (see below).

This difference between the two stability concepts consequently leads to different evaluations of the stability of mathematical models of biological communities. Consider the generalization of the Lotka-Volterra model (9) to *n*-species:

$$\frac{dx_i}{dt} = x_i(r_i - \sum_{j=1}^{n} \gamma_{ij} x_j); \tag{13}$$

where r_i designates the intrinsic growth rate of species i; γ_{ij} designates the effect of species j on species i; and $1 \leq i,j \leq n$. Equation (13) can represent several realistic features of biological communities. The γ_{ii} designate intraspecific interactions and the γ_{ij} ($i \neq j$) can represent any type of interspecific interaction: predator-prey $\gamma_{ij}\gamma_{ji}<0$, competition $\gamma_{ij}, \gamma_{ji}<0$, mutualism $\gamma_{ij}, \gamma_{ji}>0$, *etc*.

Two kinds of systems, called "conservative" and "dissipative," have been studied with (13) and highlight the difference between ecological and Lyapunov stability particularly clearly. If:

$$\sum_{i,j=1}^{n} \gamma_{ij} x_i x_j \geq 0; \tag{14}$$

the system is dissipative with strict inequality, and conservative with equality. Informally, equation (14) says interspecific interactions do not influence total

community dynamics in conservative communities and retard them in dissipative communities. Dissipative and conservative communities, Logofet (1993) suggests, are analogous to mechanical systems with and without friction.

In conservative (dissipative) communities: (i) $\gamma_{ii}=0$ ($\gamma_{ii}>0$) for all i; and, (ii) $\gamma_{ij}=-\gamma_{ij}$ for all $i\neq j$. (i) entails there is intraspecific self-damping in dissipative communities, and none in conservative communities. (ii) entails the communities only exhibit antisymmetric interspecific predator-prey interactions. Note that equation (13) is not necessarily a two trophic level model of $\frac{n}{2}$ predators and $\frac{n}{2}$ prey. Species i may be the predator and prey of different species, and part of k-length ($k\leq n$) food chains.

The direct method shows $\mathbf{x}^*$ is a nontrivial equilibrium, *i.e.* $(\forall i)(x_i^* > 0)$, of conservative n-species community models iff $\mathbf{x}^*$ is globally Lyapunov stable; it is asymptotically and globally Lyapunov stable iff the community model is dissipative. These results only hold, however, if n is even. As an indication of what defining ecological stability as global Lyapunov stability would require of communities modeled by (13) and (14), this restriction seems arbitrary and counterintuitive. Without any empirical evidence or a biological reason to suppose there is a relationship between evenness or oddness of species richness

and ecological stability, of which there seems to be none, this requirement is unreasonable.[99]

A second, more revealing feature of these results is their dependence on the exact anti-symmetry of $[\gamma_{ij}]$. If jeopardized even slightly, they no longer hold and the system may become unstable. Small changes in values of these parameters caused by realistic but weak perturbations may therefore undermine asymptotically globally stability and initiate instability (Levin 1981). This occurs because Lyapunov stability defines stability strictly in terms of system behavior after changes to *variables*, not after changes to *parameters* as well. For this reason, asymptotic global stability and weaker Lyapunov stability concepts poorly define ecological stability.

The disparity between what the direct method says about the stability properties of biological communities and what ecological stability seems to require is not limited to conservative and dissipative models of communities. A wide range of community models the direct method shows are asymptotically stable in nonlocal domains are similarly sensitive to slight changes in parameters (see Hallam 1986 and references therein).

In general, therefore, Lyapunov stability inadequately captures the idea that ecological stability depends on community response to perturbation because

[99] Of course, it is possible such a relationship exists, but has not yet been found. Most ecologists highly doubt this claim. May (1974, 53), for instance, suggested it, "border[s] on the ridiculous," and Volterra, who first recognized the fact, was similarly skeptical (Scudo 1971).

it inadequately represents real-world perturbations. As such, Lyapunov stability fails to capture principal features of ecological stability like resilience and tolerance. With respect to abiotic P_p perturbations such as temporary temperature or precipitation anomalies, for instance, resilience and tolerance cannot be assessed using Lyapunov's direct (or indirect) method (see §2.4). Temporary changes in model parameters representing these environmental variables, not changes to model variables, best represent these types of perturbation. Resilience and tolerance should be gauged by the subsequent changes in variables caused by these parameter changes. Specifically, in more resilient systems, variables return more rapidly to preperturbation values following temporary changes in parameters. Similarly, the greater the parameter change the system can sustain and have its variables return to equilibrium, the more tolerant it is. Lyapunov stability, however, cannot represent these features of ecological stability properly because it cannot correctly represent community responses to perturbations that affect factors represented by model parameters (P_p perturbations) rather than model variables (P_v perturbations).

With respect to the account of concept determination defended in Chapter 3, this failure can be understood in two related ways. First, since many, if not most, perturbations affect factors represented by parameters as well as variables, it seems to show defining ecological stability as Lyapunov stability fails the similarity criterion. A critical part of the pre-theoretic concept of ecological

stability, it might be argued, is that the concept describes a community's response to such perturbations. The imprecision of the pre-theoretic concept somewhat dilutes the overall cogency of this claim, but the failure clearly constitutes a violation of the fruitfulness criterion (see Ch. 3, §3). It reveals, specifically, that defining ecological stability as Lyapunov stability would preclude using the former in accounts of communities' responses to many, if not most, ecological perturbations. In addition, since tolerance and resilience of biological communities depend upon how communities respond to perturbations that affect model variables *and* parameters, they therefore cannot be defined in terms of properties of Lyapunov functions (see §2.3). Whereas Lyapunov stability focuses strictly on system behavior in *state* space, ecological stability essentially concerns system behavior in *parameter* space as well. Consequently, Lyapunov stability is not a sufficient condition for ecological stability, as some ecologists have explicitly suggested (*e.g*. Logofet 1993, 109) and many ecologists assume.

2.6. **Conclusion**.

That ecological stability should not be defined as Lyapunov stability does not entail the latter should play no role in mathematical modeling of biological communities. For a community at equilibrium, asymptotic Lyapunov stability within nonlocal attraction domains adequately represents ecologically stable response behavior of biological communities to perturbations that alter population

sizes of community species but leave community structure and parameter values unchanged. Lyapunov stability is therefore a plausible necessary condition for ecological stability. Moderate culling of populations in some communities or temporary cessation of plant or animal harvesting in ecosystems where it has a long history are plausible examples of such perturbations. In fact, the effects fishing cessation during WWI would subsequently have on fish populations motivated Volterra to begin developing mathematical models of biological communities (Scudo 1971).

This analysis also does not detract from the obvious gains in precision, rigor, and other scientific virtues afforded by dynamic systems modeling within ecology. It does expose, however, a limitation of the stability definition that usually accompanies this type of modeling. If ecological systems like communities were completely analogous to systems studied within applied mathematics for which Lyapunov's methods are so successfully applied, defining ecological stability as Lyapunov stability would be entirely justifiable. Section 2.5 makes clear there is, however, a crucial difference in how perturbations should be represented in the two contexts. Scientific definitions that make an initially vague concept precise by integrating it into a systematically developed mathematical theory, even one fruitfully utilized in other sciences, are therefore not always satisfactory.

Within classical mechanics, for example, force fields governing interactions between bodies, such as gravitation, are usually invariant. Masses of bodies in the system, overall system structure (*e.g.* mass-spring system, damped pendulum, mass-pulley system on an inclined plane, *etc.*), and other system features are also usually held or assumed fixed in this framework. Model features representing these system properties, such as parameter values and model structure, are correspondingly fixed. With the background held constant in this way, perturbations are represented by temporary finite changes in model variable values, for example, by displacements of position vectors and alterations to velocity vectors. Energy is conserved or monotonically dissipated for these systems depending on whether they are closed or open, so Lyapunov functions can always be constructed for them and their stability properties evaluated. Since perturbations of such systems are not taken to change the system properties represented by parameters and model structure, Lyapunov stability captures the important stability properties of these systems.

Within ecology, however, parameters representing external factors affecting species and their interactions are much more likely to change than in systems studied within classical mechanics because they are regularly altered by real-world perturbations.[100] An appropriate definition of ecological stability

[100] The difference between ecological systems and those studied in physics generally should not be overstated, however. In fluid mechanics, for instance, the background structure of the systems studied is highly variable. For the reasons discussed in section 5, therefore, Lyapunov stability would not be an appropriate representation of the stability of these systems.

therefore requires integrating Lyapunov stability with a concept representing how communities respond to these types of structural change: a structural stability concept. This would adequately account for how communities respond to real-world perturbations represented by temporary changes in variable *and* parameter values. Resilience and tolerance to real-world perturbations would be representable with such a concept.

This suggestion poses a formidable challenge to mathematical ecologists because structural stability is a much more technically complex mathematical concept than Lyapunov stability (see Peixoto 1959). The dearth of biologically-oriented work devoted to structural stability concepts (Lewontin 1969; May 1974), however, may explain its lack of application within mathematical ecology, not any essential mathematical intractability of applying the concept within ecology.

The first prominent mathematical ecologists, Lotka and Volterra, were physicists by training and this significantly influenced their approach to modeling biological systems (Kingsland 1995). Their work, moreover, subsequently set much of the agenda of twentieth century mathematical ecology. Not surprisingly, most mathematical ecologists have used the concept of Lyapunov stability and the direct and indirect methods to analyze community models. A stability concept that incorporates structural stability, however, constitutes a more defensible definition of ecological stability, and would better characterize the dynamics of ecologically

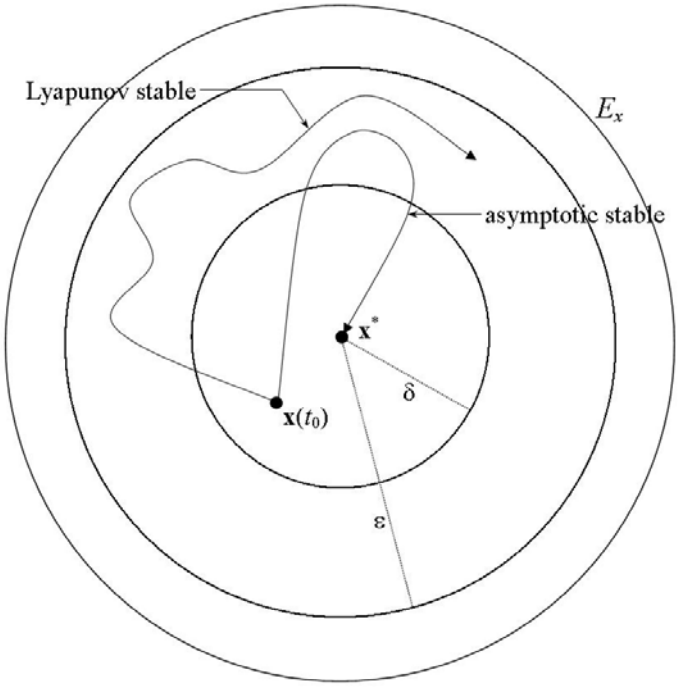
stable biological communities.

Table 1. Different concepts of ecological stability. R designates a reference state or dynamic. P_v designates perturbations to system variables; P_p designates perturbations to parameters; and, P_{vp} designates perturbations that affect both variables and parameters.

	Type	**Definition**	**Properties**
Perturbation-based Stability Types	Resilience	Rate a system returns to R following P_v, P_p, or P_{vp}. (Rosenzweig and MacArthur 1963)	comparative concept
	Resistance	Inverse of the magnitude a system changes relative to R following P_v, P_p, or P_{vp}. (MacArthur 1955)	comparative concept
	Tolerance	Range of P_v, P_p, or P_{vp} a system can sustain and still return to R. (Patten 1961)	comparative concept
	Local Asymptotic Lyapunov Stability	A system returns to R following "small" P_v. (Hirsch and Smale 1974)	(i) dichotomous concept (ii) special case of tolerance
	Global Asymptotic Lyapunov Stability	A system returns to R following any P_v. (Hirsch and Smale 1974)	(i) dichotomous concept (ii) special case of tolerance
	Structural Stability	1. small changes in parameters produce small changes in system dynamics (Lewontin 1969) 2. continuous changes in parameters produce topologically isomorphic system dynamics (May 1974)	dichotomous concept

Perturbation-independent Stability Types	Constancy	Inverse of the variability of a system. (Tilman 1999)	comparative concept

Figure 2. Graphical representation of nonasymptotic and asymptotic Lyapunov stability.



CHAPTER 5: CONCEPT DETERMINATION WITHIN ECOLOGY: ECOLOGICAL COMPLEXITY AND DIVERSITY

1. **Introduction**.

Some biological communities are more complicated than others. For instance, tropical communities usually contain more species (Pianka 1966; Willig *et al*. 2003), their species are thought (by some) to interact more intensely (Janzen 1970; Møller 1998), these interactions are more variegated in form (Dyer and Coley 2001), and they exhibit more trophic levels than tundra communities (Oksanen *et al*. 1981; Fretwell 1987). Ecologists often use two concepts, diversity and complexity, to represent differences in the "complicatedness" of communities; specifically, tropical communities are often said to be more *diverse* and/or more *complex* than tundra communities.

At a coarse level of description, the vague connotations that accompany the terms 'diversity' and 'complexity' adequately capture the imprecise judgments that some communities are more complicated than others. Disagreement arises, however, over how the two concepts should be operationalized. As early as 1969, for example, Eberhardt (1969, 503) characterized the ecological literature on diversity as "a considerable confusion of concepts, definitions, models, and measures (or indices)." MacArthur (1972, 197) similarly suggested that the term 'diversity' should be excised from ecological vocabulary as doing more harm than good, and that ecologists had, "wasted a

great deal of time in polemics about whether [Simpson's] or [Shannon's] or $\frac{N!}{N_1!N_2!...N_n!}$ or some other measure is 'best'."[101] As these remarks indicate, ecologists have proposed several mathematical measures that differ about what properties are given priority over others in assessing diversity and which differ in mathematical form. Disagreements about these issues raise the question of what properties of a community *should* be considered part of its diversity or complexity and, in turn, what adequacy conditions these concepts *should* satisfy. This chapter attempts to answer this question.

The chapter first considers the concept of the ecological diversity of a biological community. Following the strategy proposed by Sarkar (2007) for analyzing the concept, Section 2 proposes seven adequacy criteria for the concept and argues that some of those found in the ecological literature are untenable. The focus is on adequacy criteria for indices, such as Shannon's and Simpson's, that make no assumption about the underlying distribution of individual organisms among species in a community. For this reason, these indices are sometimes called *non*parametric (e.g Lande 1996) to distinguish them from indices derived from parameters of statistical models of species abundance, such as the log series (Fisher *et al*. 1943) and log normal (Preston 1948), or from biological models, such as the broken stick and overlapping niche model (MacArthur 1957).[102]

[101] See Sections 3 and 4 for a discussion of these diversity measures.
[102] See Preston 1962a, 1962b, May 1975, and Rosenzweig 1995 for reviews.

Unlike parametric indices, nonparametric diversity indices are applicable to any biological community, and since the stability-diversity-complexity debate concerns all communities, nonparametric indices are the appropriate focus of diversity here.[103] The analysis also assumes that communities have been exhaustively sampled, thereby avoiding complex issues about the adequacy of diversity indices given imperfect and incomplete sampling to focus on the problem of specifying the concept of ecological diversity when complete knowledge about the community's properties is available.[104]

Like most ecological literature on the concept of diversity, the primary focus of the chapter is on species richness and evenness as components of diversity, although issues about how other information (*e.g.* taxonomic information) should be integrated into diversity are occasionally touched upon. A myriad of diversity indices that combine species richness and evenness exist in the literature, the two most popular being Simpson's and Shannon's. Sections 3 and 4 describe these two indices and evaluate how they fare against the adequacy criteria described in Section 2. Despite its greater popularity, Shannon's index performs worse on these criteria than Simpson's. Section 5 presents a table of these and less popular diversity indices found in the ecological literature, and

[103] In fact, Lande (1996, 5) suggests that being nonparametric, and thus applicable to all biological communities, is a defensible adequacy condition for a diversity index. Moreover, some ecologists have also criticized that there is no theoretical justification for statistical models of species abundance distribution, and only poor ones for most biological models (Krebs 1989, Ch. 10).
[104] See Horn 1966; Pielou 1975, 1977; and Patil and Tallie 1982a for extensive discussions of these issues.

assesses an influential criticism of the role of the concept of diversity within ecology due to Hurlbert (1971).

The last section considers the concept of the ecological complexity of a biological community. Diversity and complexity are similar properties and may be strongly positively correlated, but they are not identical. Species of a highly diverse community may interact little and therefore exhibit low complexity, and *vice versa*. After explaining why the formulation of a quantitative complexity index is straightforward for models of biological communities in which linear differential equations represent community dynamics, Section 6 describes the significant difficulty involved in devising a complexity index for nonlinear models of communities. Since the mechanisms responsible for community dynamics – interactions within and between species in a community – are undoubtedly nonlinear, this reveals a serious problem with evaluating stability-complexity relationships in ecology.

2. **Adequacy Criteria for the Concept of Ecological Diversity**.[105]

Like most systems studied in science, biological communities can be represented with different degrees of specificity. With low representational specificity, a community can be represented in terms of the species it contains and

[105] The analysis in this section follows the strategy for analyzing the concept of ecological diversity which focuses on formulating adequacy conditions originally proposed by Sarkar (2007).

how individual organisms of the community are distributed among these species.[106] This information is provided by the *proportional species abundance vector*, V_p, of a community:

(1) $V_p =< p_1,..., p_i,..., p_n >;$

in which n designates the number of species in the community, *i.e.* its *species richness*; p_i designates the proportional abundance of the i-th species in the community; the p_i are ordered from most to least abundant (ties broken by random selection), *i.e.* $p_1 \geq ... \geq p_i \geq ... \geq p_n;$ and $\sum_{i=1}^{n} p_i = 1.$ Notice that the only properties of species V_p represents are their proportional abundances. Functional, trophic, and taxonomic differences (besides the species level) are not represented by V_p. Proportional abundances of species in a community often change over time for a variety of reasons (*e.g.* migration, interspecific interactions such as predation, competition, *etc.*) so V_p must be updated as communities change.

'Abundance' is an ambiguous term. Besides referring to the number of individual organisms of a species (a discrete variable), it can also refer to their biomass (a continuous variable). Accordingly, p_i can designate either (i) the proportion of individuals of species i in a community, such as the proportion of

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[106] Greater representational specificity is achieved, for example, if interactions between species in a community are described with differential or difference equations in addition to how individuals are distributed among species (see Ch. 4, Section 1 and Justus 2006).

wolves in an island community, given by $\frac{N_i}{N}$ where N_i is the number of individuals of species *i* and *N* is the total number of community individuals; or, (ii) species *i*'s proportion of total community biomass, such as dry weight of a particular plant species in a forest community. p_i may differ significantly on these two interpretations, so ideally V_p should be calculated according to both interpretations for a given biological community. However, for some species, such as clonal plant species or some asexually reproducing marine species, it is unclear how to count individual organisms so the biomass interpretation of p_i is preferable.

Mathematically, of course, components of V_p could take values of zero to represent species with zero abundance. Unlike species for which $p_i > 0,$ adding or subtracting these species from V_p need not change the other proportional abundances to ensure $\sum_{i=1}^{n} p_i = 1.$ Biologically, however, species for which $p_i = 0$ cannot be part of the community represented by V_p. To be one of the species comprising a community, the community must contain at least one individual of that species. As a biological collection, to deny this stipulation for communities would commit one to the idea that a community can be represented to contain a species not instantiated by any of its members. Depending on the interpretation of p_i (see above), in the following I therefore assume $p_i \geq \frac{1}{N}$ or $p_i \geq \frac{b_i}{B}$ for all *i*,

where N designates the total number of individuals in the community, B designates the total community biomass, and b_i designates the minimum biomass of an individual of species i.[107] Of course, in modeling contexts with different goals, such as in studies of extinction processes, it may be useful to allow zero components of V_p to represent when species have gone locally extinct. Similarly for species that have emigrated completely from a community. Once a species disappears from a community, however, it is no longer part of the community and does not contribute to the community's diversity.[108]

Ecologists widely agree that at least two independent properties of a community should be part of its diversity: *species richness* and *evenness* (Pielou 1966, 1975, 1977; Tramer 1969; Patil and Taillie 1982a, 1982b; Margurann 1988, 2004).[109] For a clearer understanding of these concepts, consider two simple communities, A and B, both composed of two species s_1 and s_2. A and B have the same species richness (two). If the proportions of individuals distributed among the two species are $p_1 = 0.02\%$ and $p_2 = 99.98\%$ for A and $p_1 = 50\%$ and $p_2 = 50\%$ for B, B is said to be more even than A.

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[107] For expositional convenience, only interpretation (i) from above will be discussed in the following unless otherwise specified.

[108] Alternatively, the stipulation against zero p_i could be rejected with the proviso that species richness is determined by the number of nonzero p_i in V_p. I owe Sahotra Sarkar for stressing the importance of making this option clear.

[109] McIntosh (1967) was probably the first to coin the term 'species richness' to refer to the number of species in a community. 'Evenness' and 'equitability' are used interchangeably in the ecological literature (*e.g.* Lloyd and Ghelardi 1964; McIntosh 1967; Tramer 1969; Peet 1974, 1975).

The widespread beliefs that species richness and evenness are components of diversity reflect intuitive constraints on the concept that can be formulated as explicit adequacy conditions. Specifically:

(A1) for a given evenness, diversity should increase as species richness increases (*i.e*. as *n* from [1] above increases); and,
(A2) for a given species richness, diversity should increase as evenness increases.

Note that neither (A1) nor (A2) necessitate a particular mathematical form to the increase in diversity required.

The first condition codifies an incontestable feature of the diversity concept: the diversity of a collection increases as the number of different types of entities in the collection increases. Applied to a biological collection such as a community, (A1) therefore captures the intuitive idea that a community composed of one thousand species is more diverse than one composed of ten.

There is a difficulty with (A1) as formulated, however. Unlike the clause "for a given species richness" in (A2), (A1) contains a qualification, "for a given evenness," for which V_p does not provide a quantitative characterization.[110] The problem is that increases in species richness necessitate changes in the p_i of V_p since the p_i must sum to unity following any change in species richness. This does not *necessitate* a change in evenness, but absence of a quantitative

[110] *n* from (1) provides a quantitative characterization of species richness.

characterization of evenness makes it unclear how evenness can remain static as species richness changes.[111] To avoid this difficulty, (A1) is often formulated as:

(A1′) of two maximally even communities, the more species rich community is more diverse (Pielou 1975, 7).

A quantitative characterization of 'maximally even' is provided by (A3) below.

To motivate the second condition consider two communities, each composed of 100 species and 10 000 total individual organisms. A community in which there are 100 individuals of each species seems more diverse than one in which there are 9901 individuals of one species and one individual each of the other 99. The reason seems to be that besides a consideration of the number of types of entities in a collection, diversity also involves a consideration of how well they are represented in it. For this reason, diversity is often equated with the *apparent* or *effective* number of species present in a community (*e.g*. Hill 1973; Peet 1974). For instance, to an external observer with imperfect faculties of perception, or an ecologist with insufficient time, money, and employing sampling methods with unavoidable limitations, the first community with evenly distributed individuals will usually appear to contain more species than the second community, even though they share the same species richness.[112] In this way,

[111] Similarly, although the simple example discussed above (and below) provides an informal grasp of how communities can differ in evenness, absence of a quantitative characterization also makes the clause "as evenness increases" of (A2) unclear. The remainder of this section proposes adequacy conditions which help precisify the evenness concept.

[112] A different line of thought also motivates (A2). A biological community is a set of organisms of different species. Sets are characterized by properties of their members. Members of an uneven community poorly represent some species, while each species of an even community is equally

(A2) captures the intuitive idea that community B is more diverse than community A from above.

Thus far, evenness has not been explicitly characterized and (A1) and (A2) place no constraints on the concept. Evenness is clearly maximized for a given species richness, however, when individuals of the community are equally distributed among species, *i.e.* when $p_i = \frac{1}{n}$ for all *i*. This constraint on evenness corresponds to another adequacy condition for diversity:

(A3) for a given species richness, diversity is maximal when individuals of the community are distributed equally among species (*i.e.* when evenness is maximal).

For future reference, let $V_p^{\max}$ designate the maximally even proportional species abundance vector for a given species richness.

Similarly, diversity is clearly minimized when individuals of a community are maximally unequally distributed among species. Specifically, diversity is minimal when all but (n – 1) of the individual organisms comprising the community are of one species and the rest are equally distributed (one each) among the other (n – 1) species, *i.e.* when $p_1 = \frac{N-(n-1)}{N}$.[113] This constraint can also be formulated as an explicit adequacy condition for diversity:

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represented by its members. As a set, the characterization of a community with evenly distributed individuals therefore depends more significantly on a greater number of species-types than an uneven community.

[113] Recall from above that lower case n designates numbers of species and upper case N designates numbers of individual organisms.

(A4) for a given species richness, diversity is minimal when individuals of the community are distributed maximally unequally among species (*i.e.* when evenness is minimal).

For future reference, let $V_p^{\min}$ designate the minimally even proportional species abundance vector for a given species richness.

Adequacy conditions (A1)–(A4) are found throughout the ecological literature (Hill 1973; Pielou 1975, 1977; Magurran 1988, 2004; Lande 1996; Sarkar 2007). Building on (A2)–(A4), however, a further constraint on the concept of evenness, and thus on diversity, can be formulated. Focusing on (A3),[114] if evenness is maximal for $V_p^{\max}$, evenness must decrease as V_p diverges from it. This decrease can be quantified in many ways. One rationale for doing so, however, restricts the range of possible methods of quantification. Recall that the only differences between species being considered are their proportional abundances; V_p does not represent taxonomic, trophic, functional, and other interspecific differences. Besides their proportional abundances, species are therefore being treated as equally important in assessing the diversity of a community. Thus, if evenness decreases because one species in a community deviates from its maximally even proportional abundance $(\frac{1}{n})$, for example if its

[114] Similar reasoning applies for (A4).

proportional abundance decreases to $\frac{1}{2n}$,[115] an equal deviation from the maximally even proportional abundance by another species should induce an identical decrease in evenness and thus in diversity. Formulated as an explicit adequacy condition:

(A5) for a given species richness, if V_p^i and V_p^j are proportional species abundance vectors that deviate from $V_p^{\max}$ because species *i* and species *j*, respectively, deviate equally from a $\frac{1}{n}$ proportional abundance, evenness decreases by the same amount in both cases.

Put informally, (A5) stipulates that assessment of diversity is blind to species identity. It thereby captures the frequently made assumption that the evaluation of diversity requires treating species as equals (Magurran 2004, 11). Only the extent a species' proportional abundance deviates, not what species it is, is relevant when assessing the diversity of a community.[116] (A5) is neutral, however, about whether rare or abundant species are more important to the diversity of a

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[115] Other species' proportional abundances are assumed to change uniformly so that $\sum_{i=1}^{n} p_i = 1$. This assumption is made in the following unless specified otherwise.

[116] Strictly speaking, (A5) follows from the way V_p is constructed. Recall that the p_i are ordered from most to least abundant. This was intended to impose a nonarbitrary ordering on the components of V_p. It also entails, however, that V_p^i and V_p^j referred to in (A5) are identical because p_i and p_j would fall at the same place in the ordering for V_p^i and V_p^j, respectively. If the ordering constraint were not imposed and species were assigned indices in V_p prior to determination of their proportional abundances, (A5) would constitute an independent requirement on diversity. As is, (A5) is retained to make what it requires explicit. I owe this incisive observation to Samir Okasha.

community. It requires merely that *equal* increases in the rarity of two species necessitate *equal* decreases in diversity.

Even with this further constraint, (A1)–(A5) are weak adequacy conditions for diversity in the sense that they do not determine a unique quantitative measure of diversity. In fact, many common quantitative indices satisfy these adequacy conditions (see §§3–5). Distinct quantitative diversity indices result from different ways of integrating and quantifying species richness and evenness consistent with (A1)–(A5). Before discussing the two most common such indices in the next sections, it is therefore important to consider whether any other reasonable adequacy conditions would necessitate a particular quantitative index of diversity.

Notice that (A5) does not entail different *types* of deviations from $V_p^{\max}$ (or $V_p^{\min}$), such as those involving different numbers of species, must be accorded the same import for diversity. Of course, *un*equal deviations of the same type should necessitate different values of diversity. Consider, for example, the type of deviation in which one species *i* deviates from $\frac{1}{n}$. If p_i decreases from $\frac{1}{n}$ to $\frac{1}{2n}$, diversity should decrease less than if p_i decreases to $\frac{1}{3n}$ all else being equal because the decrease in evenness is greater in the latter case (see [A2]). If p_i decreases from $\frac{1}{n}$ to $\frac{1}{4n}$, however, (A5) entails nothing about whether diversity

should decrease more or less than in a case in which p_i decreases from $\frac{1}{n}$ to $\frac{1}{2n}$ and some other p_k decreases from $\frac{1}{n}$ to $\frac{1}{2n}$.

What's needed is an method for evaluating evenness that would adjudicate between different types of deviations from $V_p^{\max}$ (or $V_p^{\min}$) for a given species richness. One natural method for doing so simply evaluates the evenness of V_p in terms of the distance from $V_p^{\max}$. A function $d : G \times G \rightarrow \mathbf{R}$ is a distance metric if it possesses three properties for all $x, y, z \in M$:

(P1) $d(x,y) \geq 0$, and $d(x,y) = 0$ if and only if $x = y$;

(P2) $d(x,y) = d(y,x)$ (symmetry); and,

(P3) $d(x,z) \leq d(x,y) + d(y,z)$ (triangle inequality) (Kaplansky 1977).

Of course, an infinite number of different functions satisfy these conditions and could therefore be used to measure deviation of V_p from $V_p^{\max}$. For instance, an especially simplistic distance metric that satisfies (P1)–(P3) is $d(x,y) = 0$ if $x = y$, and 1 otherwise, which is plainly inappropriate as a metric for measuring the distance between biological communities represented by V_p and $V_p^{\max}$.[117]

[117] According to this metric, for instance, communities A and B from above are at the same distance from $V_p^{\max}$.

Since components of V_p and $V_p^{\max}$ take real values so that they are vectors within n-dimensional Euclidean space $\mathbf{R}^n$ (*i.e.* G from above is $\mathbf{R}^n$), an appropriate distance metric, and certainly the most common, is the Euclidean metric:

(2) $$d(V_p, V_p^{\max}) = \sqrt{\sum_{i=1}^{n}\left(p_i - \frac{1}{n}\right)^2}.$$[118]

Measured in this way, evenness of a community is inversely related to the Euclidean distance between its species abundance vector and $V_p^{\max}$, where evenness is maximal.[119] For example, if the diversity of $V_p^{\max}$ and $V_p^{\min}$ for a given species richness are set at 1 and 0, respectively (see [A3] and [A4] above), the diversity of a community represented by V_p would take values on [0,1] determined by the Euclidean distance (2) between V_p and $V_p^{\max}$. Species abundance vectors that deviate from $V_p^{\max}$ in different ways but at the same distance from it would thereby have the same evenness; those at different distances from $V_p^{\max}$ would have different evenness. In particular, for the two species abundance vectors discussed above, one in which p_i for one species decreases from $\frac{1}{n}$ to $\frac{1}{4n}$ and another in which p_i and p_k for two species decrease

[118] Note that I am not claiming the Euclidean is *uniquely* defensible.

from $\frac{1}{n}$ to $\frac{1}{2n}$, the latter would be accorded greater evenness because its distance from $V_p^{\max}$ is smaller than the former.

This requirement can be codified in an explicit adequacy condition:

(A6) for a given species richness: (i) evenness decreases (increases) as the Euclidean distance from $V_p^{\max}$ ($V_p^{\min}$) increases; and, (ii) communities represented by species abundance vectors at the same Euclidean distance from $V_p^{\max}$ (or $V_p^{\min}$) have the same evenness.[120]

Similar to the way in which (A5) stipulates that diversity is blind to species identity, (A6) stipulates diversity is blind to the type of deviation from $V_p^{\max}$ (or $V_p^{\min}$). (A6) does not necessitate a unique quantification of evenness and thus diversity because the decrease (or increase) required in the first clause of (A6) may take many mathematical forms (*e.g.* concave vs. convex, linear vs. nonlinear, exponential vs. nonexponential, *etc.*). Note that (A6) can hold only if (A5) does as well.

Together with (A2), however, (A6) imposes a significant constraint on the diversity concept. It requires treating changes in the proportional abundances of

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[119] Similarly, since evenness is inversely related to the Euclidean distance, evenness is directly related to the Euclidean distance from $V_p^{\min}$.

[120] Since Euclidean distance is not the only defensible distance metric (see footnote above), (A6) need not be formulated with the former. I focus on Euclidean distance because it is the most common metric for $\mathbf{R}^n$ and clearly defensible.

rare and common species as equally important to diversity. According to (A6), for instance, diversity must decrease the same amount with a decrease in p_i for an extremely rare species and with an identical decrease in a much more common species.[121] Thus, (A6) precludes diversity from being partially sensitive to the proportional abundances of rare or common species, unlike some common diversity indices in the ecological literature (see §4), and thereby captures the same idea underlying (A5): that diversity requires treating all species as equals.

Similarly, (A6) imposes a symmetry constraint on diversity because it requires that species abundance vectors in which several species are very abundant and a few are very rare, and in which several species are very rare and a few are very abundant have the same diversity if their distances from $V_p^{\max}$ are identical. Consider, for instance, two species abundance vectors $\left\langle \frac{8}{15}, \frac{4}{15}, \frac{3}{15} \right\rangle$ and $\left\langle \frac{7}{15}, \frac{6}{15}, \frac{2}{15} \right\rangle$ with the same species richness (three). The first contains one abundant species and two rarer species (the maximally even p_i for each species is

[121] This holds for common species with proportional abundances $< \frac{1}{n}$. For common species with proportional abundances $> \frac{1}{n}$, evenness will increase as their proportional abundances decrease towards $\frac{1}{n}$.

$\frac{1}{3}$), and the second contains two abundant species and one rare species. The distances between each vector and V_p^{max}, however, are identical and hence both are accorded the same evenness and hence diversity by (A6).[122]

For the same reason diversity should be blind to species identity (see [A5]) and blind to the type of deviation from V_p^{max} (or V_p^{min}) (see [A6]), it also seems reasonable that diversity should not be partial to particular distances between V_p and V_p^{max} (or V_p^{min}) in the sense that diversity should decrease *uniformly* (*i.e.* linearly) as the distance between V_p and V_p^{max} increases. This can be formulated as an explicit adequacy condition :

(A7) for a given species richness, evenness decreases (increases) *linearly* as the Euclidean distance between V_p and V_p^{max} (or V_p^{min}) increases.

(A7) requires equal intervals of distance (as measured by equation [2]) to correspond to equal differences in diversity values, regardless of the distance between V_p and V_p^{max}. Specifically, if $d(V_p^i, V_p^{max}) = x$ and the difference in diversity value between V_p^i and V_p^{max} is y, then if $d(V_p^j, V_p^{max}) = x$ as well, the difference in diversity value between V_p^j and V_p^{max} is also y. Note that (A7) obtains only if (A6) does as well.

[122] Smith and Wilson (1996, 79) suggest a similar adequacy condition for indices of evenness.

(A6) and (A7) both follow from an underlying principle sometimes mentioned in discussions of ecological diversity (*e.g.* Krebs 1989; Magurran 2004). The principle is that diversity should not be partial among individual organisms, just as it should not be partial among species in a community. Specifically, in assessments of diversity, individual organisms should contribute to diversity in proportion only to the proportional abundance of the species to which they belong. If different types of deviations from $V_p^{\max}$ are weighted differently than as dictated by equation (2) in assessing diversity, *i.e.* (A6) is violated, some individuals will contribute more (or less) to diversity merely because they are a member of a species that has deviated from $\frac{1}{n}$ in a way favored (or disfavored) by the candidate diversity index. Similarly, if different distances from $V_p^{\max}$ are weighted differently in assessing diversity, *i.e.* (A7) is violated, some individuals will contribute more (or less) to diversity merely because they are a member of a species with a proportional abundance at a distance from $\frac{1}{n}$ that is favored (or disfavored) by the candidate diversity index. In either case, individual organisms would not be treated as equals in determining the diversity of a community composed of them.[123]

[123] There can be reasons to treat individuals of different species differently. Individuals of rare species (and their proportional abundances) are usually weighed more significantly in assessing the diversity of communities as the concept is utilized in conservation biology, for instance. Rare

Before evaluating some common diversity indices against (A1)–(A7) in the next section, this section concludes by considering another adequacy condition for diversity proposed by Lewontin (1972) and recently endorsed by Lande (1996).[124] It concerns the relationship between the diversity of individual communities and the diversity of sets of different communities. Specifically, if a super-collection of individuals is formed by pooling the individuals of several distinct smaller collections, the idea is that the diversity of the super-collection must be at least as great as the average diversity of the distinct collections. Applied to biological communities, this requires the diversity of the super-community $\bigcup_{i=1}^{z}\{C_i\}$ formed by pooling the individuals of each community C_i to be greater than or equal to the mean diversity of the C_i (z is an index of the communities). Stated formally:

(3) $$DIV(\bigcup_{i=1}^{z}\{C_i\}) \geq \frac{1}{n}\sum_{i=1}^{z} DIV(C_i);$$

in which equality holds only if the C_i are *compositionally* identical, *i.e.* $V_p^{C_i} = V_p^{C_j}$ for all $i \neq j$.

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species are typically more likely to go extinct. Indices that accord changes in their proportional abundances more import than changes in common species are likely favored in conservation contexts because changes in the former are more likely to influence species persistence than changes in the latter (see §§3-5).

[124] Lewontin (1972) may have been the first to formulate this as an adequacy condition for the concept of diversity.

Lewontin did not provide a rationale for this constraint on ecological diversity, called *strict concavity*, and there are reasons to reject it as an adequacy condition. To illustrate, consider two simple communities C and D composed of four different species (two each) with *absolute* (not proportional) abundances <2,2> and <1000,1000>. The absolute species abundance vector for the super community C∪D with species richness four is <1000,1000,2,2>. Equation (3) requires the diversity of C∪D be greater than the average diversity of C and D, but it is unclear why this is defensible, certainly as an adequacy condition on the concept of diversity. C∪D contains more species than either C or D, and in this respect seems more diverse. It is also, however, highly uneven compared with C or D. The proportional species abundance vector for C∪D is approximately <0.499,0.499,0.001,0.001> which is a highly uneven distribution, unlike the highly even distribution of C and D, <0.5,0.5>. Equation (3) therefore forces a strong rank order of species richness over evenness in assessments of diversity.

This *may* be a defensible property of a proposed diversity index.[125] In the context of conservation biology, for example, there may be advantages to prioritizing species richness over evenness in assessments of the diversity of communities targeted for conservation. Equation (3) is not, however, a defensible adequacy criterion for *any* potential quantitative specification of diversity. Species

[125] Note that this property is consistent with (A1)–(A7) from above, which do not compel any relationship between species richness and evenness in assessments of diversity.

richness and evenness are independent properties. Though this does not entail one is not more important than another in evaluations of a community's diversity, nothing about the pre-theoretic concept of ecological diversity seems to suggest otherwise. Pielou (1977, 292), for instance, explicitly rejected the constraint imposed by (3): "since diversity depends on two independent properties of a collection … a collection with few species and high evenness could have the same diversity as another collection with many species and low evenness."[126]

3. **Simpson's Index**.

The first index that included species richness and evenness as components of diversity found in the ecological literature was proposed by Simpson (1949). Simpson claimed that the probability two individuals drawn at random (with replacement) from an indefinitely large collection are of the same group is $\sum_{i=1}^{n} p_i^2$, where *n* is the number of groups exhibited within the collection, and he called it a "measure of concentration."[127] Applied to biological communities, $\sum_{i=1}^{n} p_i^2$ then

[126] In passing, Lande (1996, 8) motivates strict concavity as an adequacy condition by pointing out that its denial, "implies the possibility of a negative diversity among communities." But it is unclear why this is problematic. It does not, for instance, entail the diversity of any individual community is negative, which would clearly be problematic.

[127] Simpson's claim assumes the probability of selecting two individuals from the same group is directly proportional to their relative abundances, which is violated under a variety of plausible biological conditions (see below). I owe Sahotra Sarkar for highlighting this implicit assumption.

measures the dominance (in terms of abundance) of species within the community (Pielou 1977) and is at its minimal value ($\frac{1}{n}$) for a given species richness *n* when individuals of the community are equally distributed among the *n* species, *i.e.* when $V_p = V_p^{\max}$.

The complement of Simpson's (1949) measure:

(*D*) $1 - \sum_{i=1}^{n} p_i^2$, [128]

represents the probability two randomly selected individuals belong to different species, which is an intuitive measure of diversity.[129] *D* is at its maximal value for a given species richness *n* ($D = 1 - \frac{1}{n}$) when individuals are maximally equally distributed among species, *i.e.* when $V_p = V_p^{\max}$, and at its minimal value when individuals are maximally unequally distributed among species, *i.e.* when $V_p = V_p^{\min}$. This minimum is not the value of *D*, however, when all individuals of the

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[128] The inverse of Simpson's concentration measure, $\frac{1}{\sum_{i=1}^{n} p_i^2}$, is also commonly used as an index of diversity (Williams 1964; Levins 1968; Hurlbert 1971; MacArthur 1972; Hill 1973; May 1975; Pielou 1977; Magurran 1988, 2004; Lande 1996).

[129] The counterpart of *D* that does not make the idealization that the two individuals are drawn from an indefinitely large population is $1 - \sum_{i=1}^{n} \frac{N_i(N_i - 1)}{N(N-1)}$ and will not be discussed here (Pielou 1977; Magurran 2004).

community are of the same species, which is 0. $D = 0$ when all but one p_i is zero, but this set of proportional abundances violates the biological requirement on V_p that $p_i \geq \frac{1}{N}$ for all *i* stipulated above.[130]

Several ecologists have suggested a stronger, but similarly inaccurate interpretation of *D*. Hurlbert (1971), for instance, proposed that if *D* is multiplied by $\frac{N}{N-1}$ the resulting index represents the probability of interspecific encounter in the community, rather than just the probability two randomly selected individuals belong to different species. Patil and Taillie (1982a) made a similar claim and showed how quantities such as the waiting time for intra and interspecific encounter are related to *D* on this stronger interpretation. Recently, Ricotta (2000, 246) has suggested the same interpretation: "Simpson's diversity index is generally defined as the complement to the total probability of interspecific interactions in the community." This interpretation is only sound, however, if an additional assumption is made about community structure. In response to Patil and Taillie's analysis, Sugihara (1982) correctly pointed out that *D* represents the probability of interspecific interaction only if the frequencies of interspecific encounters are directly proportional to the relative abundances of the species interacting. The problem, Sugihara (1982, 565) emphasized, is that:

[130] See the discussion preceding (A4) in Section 2.

> None of these interpretations [of *D*], however, has yet proved to be very fruitful, as they suffer from such real-world concerns as spatial patchiness and clumping in species distributions, differential mobility, and problems associated with interpreting niche overlap between species from their spatial covariance. Approaching the study of species diversity through a priori models is a valid enterprise, but requires a clear intuition of how communities operate, which thus far seems to be lacking.

D may be a good *estimator* of the probability of interspecific encounter if species are spatially distributed relatively uniformly throughout the area occupied by the community. If distributed in this way, species are likely to interact in direct proportion to their abundances. But without knowing this, and without a thorough understanding of the factors Sugihara mentioned that may prevent such a distribution, the legitimacy of the stronger interpretation of *D* cannot be reliably verified.

As has been noted throughout the ecological literature, *D* satisfies (A1)–(A4) (Hill 1973; Pielou 1975, 1977; Magurran 1988, 2004; Lande 1996).[131] *D* also clearly satisfies (A5). As the similar mathematical structure of *D* and (2) from above suggest, *D* also satisfies (A6). To see this, recall that (A6) requires that: (i) the diversity of the community represented by V_p be inversely related to $d(V_p, V_p^{\max})$; and, (ii) that if $d(V_p^i, V_p^{\max}) = d(V_p^j, V_p^{\max})$ for a given species richness, the diversity of communities represented by V_p^i and V_p^j are equal.

[131] Lande (1996) also showed, furthermore, that *D* is concave (see §2) although $\frac{1}{\sum_{i=1}^{n} p_i^2}$ is not.

Diversity is directly related to – $d(V_p, V_p^{\max})$ given (i), so what is first needed is to show that D exhibits the same relationship with – $d(V_p, V_p^{\max})$. The following algebraic identities demonstrate the required relationship:

$$
\begin{aligned}
d(V_p, V_p^{\max}) &= \sqrt{\sum_{i=1}^{n}\left(p_i - \frac{1}{n}\right)^2} \\
&= \sqrt{\sum_{i=1}^{n}\left(p_i^2 - \frac{2p_i}{n} + \frac{1}{n^2}\right)} \\
&= \sqrt{\sum_{i=1}^{n}\left(p_i^2\right) - \frac{2}{n}\sum_{i=1}^{n}\left(p_i\right) + \sum_{i=1}^{n}\left(\frac{1}{n^2}\right)} \\
&= \sqrt{\sum_{i=1}^{n}\left(p_i^2\right) - \frac{2}{n} + \frac{1}{n}} \\
&= \sqrt{\sum_{i=1}^{n}\left(p_i^2\right) - \frac{1}{n}}\,.
\end{aligned}
$$

Substitution for $\sum_{i=1}^{n} p_i^2$ using the definition of D from above yields: $\sqrt{(1-D) - \frac{1}{n}}$, which equals $\sqrt{-D + \frac{n-1}{n}}$.[132] Since $\frac{n-1}{n}$ is constant and nonnegative for a given n, $d(V_p, V_p^{\max})$ decreases as D increases. Similarly, if $d(V_p^i, V_p^{\max})$ =

$d(V_p^j, V_p^{\max})$, then $\sqrt{-D_i + \frac{n-1}{n}} = \sqrt{-D_j + \frac{n-1}{n}}$ where D_i and D_j represent the complement of Simpson's index for the proportional abundances of V_p^i and V_p^j, respectively, from which it follows that $D_i = D_j$ (given that D must be positive). (A6) is thereby satisfied.[133]

That $d(V_p, V_p^{\max}) = \sqrt{-D + \frac{n-1}{n}}$ also shows, however, that D does not satisfy (A7). (A7) requires diversity decrease linearly with $d(V_p, V_p^{\max})$, but D scales quadratically with $d(V_p, V_p^{\max})$. Thus, D violates (A7) because it is more sensitive to changes in proportional species abundance vectors at greater distances from $V_p^{\max}$. In particular, D is more sensitive to the proportional abundances of especially abundant or especially rare species. If diversity were specified with Simpson's index, (A7) would therefore not be satisfied and diversity would fail to be impartial among individual organisms comprising a community.

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[132] The term $\sqrt{-D + \frac{n-1}{n}}$ is well defined because $-D + \frac{n-1}{n}$ is nonnegative. Specifically, at its maximum $D = 1 - \frac{1}{n}$, in which case $\sqrt{-D + \frac{n-1}{n}} = 0$.

[133] As a check on this result, it can be verified that the two species abundance vectors $\left\langle \frac{8}{15}, \frac{4}{15}, \frac{3}{15} \right\rangle$ and $\left\langle \frac{7}{15}, \frac{6}{15}, \frac{2}{15} \right\rangle$ from above, which have the same distance (0.3887) according to equation (2), also have the same value (0.6044) according to Simpson's index.

4. **Shannon's Index**.

Probably the most popular index of community diversity is the Shannon index (*H*), so-called after Claude Shannon, who developed it in the context of what came to be called information theory.[134] The index was originally formulated to quantify the amount of information in a communicated message (Shannon 1948; Shannon and Weaver 1949), and despite Margalef's (1958) claim to priority, Good (1953) was the first to use it as an index of ecological diversity. The index is given by:

$$(H) \qquad -\sum_{i=1}^{n} p_i \ln p_i .$$ [135]

Within information theory, *H* is used to measure the information of a message composed of *n* types of symbols whose individual probability of occurrence is p_i, $i = 1,...,n$. Within ecology, however, p_i represents the familiar proportional abundance of species *i* and *n* represents the community's species richness.

H is at its maximal value (ln *n*) for a given species richness *n* when individual organisms are equally distributed among species, thereby satisfying

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[134] Aczél and Daróczy (1975) suggest Norbert Wiener independently developed an index which is a special case of Shannon's more general index in 1948 (Wiener 1948).

[135] Shannon's index assumes p_i is a proportional species abundance from an infinitely large community (Magurran 2004). This idealization, and the emendation needed to correct it for finite communities, will not be discussed here. The sampling estimator of *H* which does not make this assumption is Brillouin's index, $\frac{1}{N}\ln\left(\frac{N!}{N_1!N_2!...N_n!}\right)$ (Brillouin 1962). Horn (1966) developed two measures of overlap between samples of communities based on Simpson's and Shannon indices, respectively.

adequacy condition (A3) (Pielou 1977). *H* satisfies (A1), (A2), and (A4) (Hill 1973; Pielou 1975, 1977; Magurran 1988, 2004; Lande 1996), and *H* obviously satisfies (A5). Compared with *D*, however, *H* is less sensitive to proportional abundances of species (and hence evenness) and more sensitive to species richness than Simpson's index *D* (May 1975; Magurran 1988, 2004).

Shannon's index is also more sensitive than Simpson's index to the abundances of rare species (Peet 1974), as a simple example demonstrates. Consider a four species community *E* composed of one abundant, one rare, and two evenly distributed species such that $V_p = <\frac{12}{32}, \frac{8}{32}, \frac{8}{32}, \frac{4}{32}>$. $D = 0.7188$ and $H = 1.3209$ for *E*. If the rare species becomes rarer, so that V_p becomes $V_p^r = <\frac{13}{32}, \frac{9}{32}, \frac{9}{32}, \frac{1}{32}>$, then evenness decreases and both *D* and *H* decrease to 0.6758 and 1.1878, respectively. If the abundant species becomes more abundant, so that V_p becomes $V_p^a = <\frac{15}{32}, \frac{7}{32}, \frac{7}{32}, \frac{3}{32}>$, then evenness also decreases and both *D* and *H* decrease to 0.6758 and 1.2420, respectively. That *H* decreases more than *D* for V_p^r or V_p^a does not necessarily show it is more sensitive to rare or abundant species because the range of values *D* and *H* take between $V_p^{\min}$ and $V_p^{\max}$ differ, so that differences in their values may be due merely to a scaling effect. The way in which values of *D* and *H* change from V_p to $V_p^{\min}$ and to $V_p^{\max}$, however, reveal

that H is more sensitive to abundances of rare species. Specifically, H decreases more between V_p and V_p^r (1.3209 – 1.1878 = 0.1331) than between V_p and V_p^a (1.3209 – 1.2420 = 0.0789), while D decreases by the same amount between V_p and V_p^r, and V_p and V_p^r. H is therefore more sensitive to the abundances of rare species than D, which is equally sensitive to either. Note that since $d(V_p^r, V_p^{\max}) = d(V_p^a, V_p^{\max})$, a diversity index should decrease by the same amount for V_p^r and V_p^a according to (A6).

Despite these and other differences (see below), Simpson's and Shannon's indices are both members of a family of entropy measures defined by: $H_q = \frac{\ln \sum_{i=1}^{n} p_i^{\alpha}}{1-\alpha}$, in which $\alpha > 0$ and $\alpha \neq 1$ (Rényi 1961; Pielou 1975). Rényi (1961) showed, for example, that $\lim_{\alpha \to 1}(H_q) = -\sum_{i=1}^{n} p_i \ln p_i = H$. Pielou (1975) showed that if $\alpha = 2$, $H_q = -\ln \sum_{i=1}^{n} p_i^2$, which is equivalent to the inverse form of Simpson's diversity index after exponential transform. Similarly, H_q is equivalent to the exponential transform of species richness (ln n) when $\alpha = 2$.

Before considering whether H satisfies (A6) and (A7), a clear *ecological* interpretation of it is needed. Pielou (1977) provided a particularly simple, and probably the clearest interpretation. As an entropy measure, Pielou suggested H

accurately measures uncertainty, and that diversity and uncertainty are closely related concepts.[136] Specifically, as the diversity of a community increases, the uncertainty about which species a randomly selected individual belongs to increases. It is difficult to deny this claim, but the crucial issue is whether H is the *uniquely* appropriate measure of uncertainty. After all, given the interpretation of D described in Section 3, it also seems to measure a similar, if not identical, kind of uncertainty about a biological community.

Pielou's argument that H is a uniquely appropriate index of ecological diversity relied on a mathematical fact about H proved in a non-ecological context by Shannon. Shannon (1948) showed that H is the only function (up to a multiplicative constant) which exhibits three properties he thought reasonable to require of the concept of information.[137] These properties include that an information function should be continuous in p_i, that it should monotonically increase with n for maximally even p_i (see [A1′] from above), and an additive property which was the basis of Pielou's argument for preferring H over other diversity indices and, even stronger, that it constitutes an adequacy condition for

[136] Pielou's view of the proper ecological interpretation of Shannon's index shifted markedly in the 1960s and 1970s. In 1966, Pielou suggested there was an "obvious analogy" between a biological community and a coded message, and that, "the actions of a biologist are formally identical with those of a man observing, one after another, the symbols of a message" (1966, 164). (A very similar characterization had been suggested by Margalef (1958) almost a decade before.) By 1975, however, Pielou's view of such analogies was decidedly negative: "it cannot be too strongly emphasized that fancied links between the information-theoretic concept of 'information' and the diversity of an ecological community are merely fancies and nothing more" (1975, 9).

[137] In a later review of information theory, Aczél and Daróczy (1975, 29) called these properties, "natural properties which are essential from the point of view of information theory." Shannon,

any index of diversity (Pielou 1977, 293-294). The interpretation of this property as applied to biological communities requires some elaboration.

Just as V_p is based on a classification P of individuals of a biological community into n species, let V_q be a proportional abundance vector with m components based on a different classification Q. The second classification could be derived from further taxonomic information, information on habitat requirements or other properties of individual organisms, *etc*. As with the p_i, assume that the proportional abundances q_j of the second classification are such that $\sum_{j=1}^{m} q_j = 1$, and that each individual organism falls into only one class. Like the information concept, if the two classifications are independent, Pielou (1977, 294) suggested that ecological diversity must satisfy:

(4) $$DIV(PQ) = DIV(P) + DIV(Q);$$

in which $DIV(PQ)$ is the diversity of a biological community with individuals classified into both P and Q for a total of $m \times n$ classes, and $DIV(P)$ and $DIV(Q)$ are the diversity of the community with individuals classified by only P or Q, respectively.[138] Mathematically, it can be shown that H is the only continuous function of the p_i up to a multiplicative constant that satisfies (A1′), (A3), and for which equation (4) holds (Khinchin 1957).

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however, only called them "reasonable" and emphasized that, "The real justification of these definitions, however, will reside in their implications," (Shannon and Weaver 1949, 50).

[138] Equation (4) can be generalized to any finite number of independent classifications.

In general, (4) is a desirable mathematical property because it permits the additive decomposition of a function of two combined input arguments. Together with its intuitive plausibility for the concept of information, this motivated Shannon (1948), Khinshin (1957), Rényi (1961), Aczél and Daróczy (1975), and others to stipulate it as an adequacy condition for any information measure. What is needed to show it is an appropriate adequacy condition for the concept of ecological diversity, however, is an account of why this is a *necessary* property of diversity, which Pielou (1977) did not supply. *If* diversity were specified as *H*, (4) logically follows given its logarithmic form, and it can be agreed that there are benefits of being able to additively decompose ecological diversity in this way (Pielou 1977, 303-307). This is insufficient, however, to establish the stronger claim that (4) is a defensible *adequacy* condition, especially given that there are other methods with attractive features in which ecological properties besides proportional species abundances can be integrated into a measure of diversity of a community (*e.g.* Rao 1982; Ricotta 2002).

It remains to assess whether *H* satisfies (A6) and (A7). Unlike *D*, *H* does not satisfy (A6). The proportional species abundance vectors $\left\langle \frac{8}{15}, \frac{4}{15}, \frac{3}{15} \right\rangle$ and $\left\langle \frac{7}{15}, \frac{6}{15}, \frac{2}{15} \right\rangle$, and $\frac{13}{32}, \frac{9}{32}, \frac{9}{32}, \frac{1}{32}$ and $\frac{15}{32}, \frac{7}{32}, \frac{7}{32}, \frac{3}{32}$ from above provide clear counterexamples. Although their distances as determined from equation (2) are

equal, their *H* values differ (1.0096 and 0.9908, 1.1878 and 1.3209, respectively). Since (A6) is a necessary condition of (A7), *H* also fails to satisfy (A7).[139]

5. **The Role of the Diversity Concept within Ecology**.

Simpson's and Shannon's diversity indices emerged within ecology in the late 1940s and 1950s. By the late 1960s, a large number of diversity indices had been formulated, and numerous empirical studies of different ecological systems were being conducted to estimate diversity using these indices.[140] Table 2 provides a list of some common diversity indices found in the ecological literature. Enough attention was being devoted to indices of diversity by the early 1970s to spark criticism, perhaps the most incisive from Hurlbert (1971). In his influential critique of this research agenda, Hurlbert (1971, 577) argued that, "the term 'species diversity' has been defined in such various and disparate ways that it now conveys no information other than 'something to do with community structure'," and that this indicated a fundamental vagueness of the underlying concept. He thought ecologists had further exacerbated this problem by appropriating statistical measures of diversity developed in nonbiological contexts, such as information theory, with dubious ecological relevance. MacArthur (1972, 197) voiced the same criticism of the concept of ecological

[139] This result complements Lande's (1996) preference for *D* over *H* on the basis that there is an unbiased estimator for *D*, but none for *H*.
[140] See Pielou 1975, 1977; Magurran 1988, 2004; Sarkar 2007; and Drake 2007 for comprehensive reviews.

diversity independently around the same time: "Applying a formula and calculating a 'species diversity' from a census does not reveal very much; only by relating this diversity to something else – something about the environment perhaps – does it become science." Other ecologists were similarly skeptical of the role of the concept of diversity within ecology, and especially of the ecological utility of information theory (*e.g.* Hill 1973).

Rather than attempt to rehabilitate the concept by proposing adequacy conditions by which to evaluate relative merits and weaknesses of different diversity indices as attempted in Section 2, Hurlbert suggested the search for relationships between diversity and other community properties, such as stability, should be refocused on the relationship between those properties and indices that reflect biologically meaningful properties that might influence community dynamics. His proposed index of the probability of interspecific encounter is one example. As a measure of ecological diversity, note that species richness alone fails this test since it is generally unlikely that extremely rare species (*e.g.* s_1 in community A from Section 2) play an important role in community dynamics.[141] Since it does not consider evenness, furthermore, species richness fares very poorly as a specification of ecological diversity; it fails adequacy conditions (A2)–(A7). Species richness was and remains, however, the predominant

[141] Potentially important exceptions include keystone species and so-called "ecosystem engineers" (see Paine 1969, Jones *et al*. 1994; and Power *et al*. 1996).

surrogate for diversity in analyses of stability-diversity relationships (*e.g*. Tilman 1996, 1999). These studies therefore offer negligible insights into possible relationships between the stability and diversity in biological communities.

Since Hurlbert's critique, ecologists have proposed a multitude of new diversity indices to satisfy different proposed adequacy conditions besides those about species richness and evenness (see Magurran 2004, Ricotta 2005, and Sarkar 2007 for reviews). Diversity indices should increase, for instance, as interspecific taxonomic and functional differences increase. Besides properties of species, spatial properties of their geographical distribution could also be included in an index of ecological diversity. Since species distributions are significantly influenced by regional geology and environmental gradients, however, including these properties would expand the scope of ecological diversity beyond just the biological properties of communities. Expanded in this way, the "diversity" of the physical environment in which a community resided would also contribute to the value of indices of diversity. However, properties of the spatial extent of species, such as their geographical rarity, are clearly relevant to the concept of diversity utilized in the context of biodiversity conservation, and therefore must be integrated into any defensible measure of biodiversity (Sarkar 2002, 2005b, 2007).

How compatible these additional adequacy conditions are with one another, or with the other conditions is not yet clear. Some conditions appear to be

conceptually independent, but some formal diversity indices suggest that others are not. Rao's (1982) "quadratic entropy" diversity index, for instance, which generalizes the Simpson index (Ricotta and Avena 2003), incorporates interspecific taxonomic and functional differences as well as evenness and species richness into a single quantitative measure. Unlike the Shannon and Simpson indices, however, quadratic entropy violates the adequacy condition (A3) that diversity should be maximal for a given species richness when individuals are equally distributed among species (Ricotta 2005). (A4) is also violated. This is as it should be. If functional or taxonomic information is included in assessments of diversity, then high functional or taxonomic diversity may make a less even community more diverse overall than a more even one. In effect, functional or taxonomic diversity can trump evenness.

As new indices are devised, similar incompatibilities between other adequacy conditions may be revealed. Absent a general proof that plausible adequacy criteria are themselves incompatible, however, the formulation of a uniquely defensible diversity index satisfying all of them remains possible. In any

case, adequacy conditions (A1)–(A7) are compatible and thus a defensible diversity measure satisfying them exists.[142]

6. **Problems with Formulating a Concept of Ecological Complexity**.

Focusing solely on diversity when considering what properties of communities may make them stable is unjustifiable because intra- and inter-specific dynamics largely determine a community's stability properties. As a function of properties of individual organisms in a community, such as what taxonomic classes they exhibit, how they are distributed among these classes, *etc*., even biologically meaningful diversity indices may reveal little about community dynamics. Individuals in species rich communities with high evenness and taxonomic variety may interact rarely and weakly (intra- and inter-specifically); thus, the former entails nothing about the latter. Hurlbert's (1971) claim that D (multiplied by $\frac{N}{N-1}$) measures the probability of interspecific encounter, for instance, is true only if individuals of different species meet in proportion to their relative abundances (Sugihara 1982). The likelihood may be higher, of course, that species in more even communities will interact more frequently, but the latter

[142] In fact, (A6) and (A7) suggest two obvious candidates: (i) $-\sqrt{\sum_{i=1}^{n}\left(p_i-\frac{1}{n}\right)^2}$; and, (ii)

cannot be inferred from the former alone. A high or low diversity does not, moreover, reveal anything about how strongly species interact. May (1974) may have focused on complexity rather than diversity for precisely these reasons.[143]

Unlike diversity, complexity is defined in terms of community dynamics. The more species, the more frequently they interact, and the stronger they do, the more complex the community. As a function of intra and inter-specific dynamics, complexity can only be assessed against a description of these dynamics, usually in the form of a mathematical model. With respect to the simple linear models analyzed by May (1974), for instance, complexity is a function of species richness (n), connectance (C), and mean linear interaction strength (s) (see Ch. 2, §4).[144] How complexity should be assessed for more complicated nonlinear models, however, is unclear. Determining species richness is obviously unproblematic, and connectance can be determined from functional dependencies between variables in the model. The problem is assessing mean interaction strength. For linear models, the growth rate of each species is a linear function of the abundances of species with which they interact, so s is simply the average of the interaction coefficients. Variables in nonlinear models, however, may interact in

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$\frac{1}{\sqrt{\sum_{i=1}^{n}\left(p_i - \frac{1}{n}\right)^2}}$, which both also satisfy (A1)–(A5).

[143] May (1974) was no explicit on this point. See Chapter 2, Section 4.

[144] May did not specify an explicit function for complexity.

disparate ways and may exhibit different functional relationships, which precludes simply averaging to determine *s*. Different methods of integrating strengths of distinct types of relationships into a single quantitative complexity value, assuming there is a defensible way of doing this, would beget different measures of complexity.

Restricting complexity to just *n*, *C*, and *s* is also unduly restrictive. The variety of relationships exhibited between variables, the number of parameters, how complicated their relations are with variables, and other properties of community models that represent important features of community dynamics should be part of any defensible measure of ecological complexity. Whether they can be codified into a general complexity index remains to be seen. Without such a codification, however, whether a relationship between ecological stability and complexity exists is a poorly formed question.

Table 2. A list of common diversity indices in the ecological literature.

Diversity Index	Mathematical Operationalization	Origin
Simpson's Index (infinite community)	D: $1-\sum_{i=1}^{n} p_i^2$ or $\frac{1}{\sum_{i=1}^{n} p_i^2}$	Simpson (1949)
Simpson's Index (finite community)	$1-\sum_{i=1}^{n} \frac{N_i(N_i-1)}{N(N-1)}$ or $\frac{1}{\sum_{i=1}^{n} \frac{N_i(N_i-1)}{N(N-1)}}$	Simpson (1949)
Shannon's index (infinite community)	H: $-\sum_{i=1}^{n} p_i \ln p_i$	Shannon (1948)
Brillouin's index (Shannon's index for a finite community)	$\frac{1}{N}\ln\left(\frac{N!}{N_1!N_2!...N_n!}\right)$	Brillouin (1962)
Margalef's Index	$\frac{n-1}{\ln(N)}$	Margalef (1958)
Menhinick's Index	$\frac{n}{\sqrt{N}}$	Menhinick (1964)
McIntosh's index	$\frac{N-\sqrt{\sum_{i=1}^{n} N_i}}{N-\sqrt{N}}$	McIntosh (1967)
Berger-Parker's index	$1-\frac{N_{\max}}{N}$ or $\frac{N}{N_{\max}}$	Berger and Parker (1970)
Hurlbert's "Interspecific Encounter" Index	$\left(\frac{N}{(N-1)}\right)\left(1-\sum_{i=1}^{n} p_i^2\right)$	Hurlbert (1971)

Fager's Index	$\frac{N(n+1)}{2} - \sum_{i=1}^{n} r_i N_i$	Fager (1972)
Hill's Family of Diversity Indices	$\left(\sum_{i=1}^{n} p_i^a \right)^{\frac{1}{(1-a)}}$	Hill (1973)
Keefe and Bergersen's Index	$1 - \frac{N}{(N-1)} \left(\sum_{i=1}^{n} p_i^2 - \frac{1}{N} \right)$	Keefe and Bergersen (1977)
Rao's "Quadratic Entropy" Index	Q: $\sum_{i,j=1}^{n} d_{ij} p_i p_j$	Rao (1982)

Glossary:

n = species richness;
p_i = the proportional abundance of species i;
N_i = the abundance of species i;
N = the abundance of all species in the community;
N_{max} = abundance of the most abundant species;
d_{ij} = distance (*e.g.* taxonomic, functional, *etc.*) between species i and j;
r_i = rank of species i in V_p;
a = a constant ≥ 0.

CHAPTER 6: CONCLUSION: EVALUATING STABILITY-DIVERSITY-COMPLEXITY RELATIONSHIPS

As with many unresolved scientific debates, the stability-diversity-complexity (SDC) debate has many facets, each of which complicates its evaluation in several ways. The first complication is that a biological community can be represented in a multitude of ways. One of the most common types of representation in ecology, and science in general, are mathematical models, rather than verbal, diagrammatic, mechanical, or other types of models. Mathematical models of biological communities take a wide array of functional forms and can contain many different types of variables. As Chapter 4, Section 1.1 showed, assessments of stability properties such as resistance, resilience, and tolerance depend upon the details of these models, and thus conclusions drawn from analyses of stability-diversity and stability-complexity relationships are limited by the type of model and variables used to represent the community, as well as the model's accuracy. Similarly, Chapter 5, Section 6 showed why the details of these models are critically relevant in assessments of a community's complexity, particularly the way in which factors that drive its dynamics are represented. Different models used to represent the same biological community may therefore exhibit different stability properties and degrees of complexity.

A second complication is that stability must be evaluated with respect to a reference state or dynamic. A wide variety of different reference states or

dynamics, however, can be specified for a biological community that reflect an intuitive sense of stability, such as a point equilibrium, a limit cycle, a more complicated attractor set, ranges of allowed fluctuation in the abundances of species comprising the community, *etc*. What state or dynamic is an appropriate reference for a given community depends partly on the state or dynamic it exhibits in the absence of perturbations, and partly on the objectives of the analysis of the community. As Chapter 4, Section 1.1 argued, stability properties of a community must be gauged against the reference state or dynamic specified for it, so different specifications for the same biological community can lead to different conclusions about its stability.

As Chapter 4, Section 1.2 showed, a third complication is that the concept of ecological stability is multifaceted, comprised of three properties: resistance, resilience, and tolerance. Since these properties are conceptually independent, they *may* be related to the complexity or diversity of biological communities in disparate ways.[145] These properties can also be operationalized with quantitative measures in numerous ways, and the value of each measure also depends upon how the biological community is represented in a model and what reference state or dynamic is specified for it.[146] Thus, besides the type of representation and reference state or dynamic specified for a community, generalizations that can be

[145] Of course, with respect to a specified system description and reference state or dynamic, dependencies may exist between quantitative measures of these properties.
[146] Operationalization is a kind of explication (see Ch. 3).

drawn from particular studies of stability-diversity and stability-complexity relationships are also constrained by the specific stability property being analyzed, as well as the measure used to quantify it.

As Chapter 5, Sections 3–5 (and Table 1 therein) showed, a fourth complication is that numerous operationalizations of ecological diversity, many with significantly different properties, have been proposed in the ecological literature. Despite this multitude of diversity indices, almost no study of stability-diversity relationships has used a defensible index of diversity, for instance, one that satisfies at least the uncontroversial adequacy conditions found in the ecological literature ([A1]–[A4]; see Ch. 5, §2). Instead, a simplistic and demonstrably unsatisfactory measure of ecological diversity, species richness, is most often used in analyses of stability-diversity relationships because the number of species composing a community is much easier to estimate empirically than the proportional species abundances required to measure its evenness (see below).

For the same reason, Chapter 4, Section 1.3 argues poor measures of ecological stability such as constancy are often used in studies of stability-diversity and stability-complexity relationships. Empirically, it is much easier to acquire data about the variability of species abundances in a community, for example, than data about properties of the community's dynamic response to perturbation, such as resistance, resilience, and tolerance. Similarly, Chapter 4, Section 2.6 explains why it is theoretically much easier to evaluate the Lyapunov

stability of a mathematical model of a community using well-developed analytic techniques than it is to evaluate the kind of structural stability required by ecological stability (see below).[147]

As might be expected for a debate with the complexity outlined above and discussed in detail in preceding chapters, the SDC debate remains unresolved after more than half a century of ecological research. Given the debate's complexity, it is also unsurprising that only a few of the total possible relationships between ecological stability, complexity, and diversity have been analyzed, or that there has been confusion about how these concepts *should* be defined and their relationships evaluated. In particular, only two relationships have been the predominant focus of research thus far: (i) the relationship between local Lyapunov stability and complexity of models representing biological communities with linear differential equations; and, (ii) the relationship between constancy of species abundances of communities and their species richness (see Ch. 2). The tractability of these concepts as compared with more defensible characterizations of stability, diversity, and complexity accounts for the selective scrutiny.

The history recounted in Chapter 2 demonstrated that the focus on these two relationships also reflects disparate approaches empirically and theoretically

[147] Though it has received little research focus in the SDC debate, structural stability could be analyzed through simulation, thereby avoiding the difficulties confronting its *analytic* evaluation. Thanks to Sahotra Sarkar for calling this possibility to my attention.

oriented ecologists have taken to the debate, as exemplified, for example, by studies such as MacArthur (1955), Elton (1958), Pimentel (1961), May (1974), and Tilman (1996, 1999). Theoretical ecologists principally focus on mathematical models of biological communities. Since these models usually describe mechanisms driving the dynamics of communities that ecological complexity depends upon but not the distribution of individual organisms among species that ecological diversity depends upon, their research has been primarily concerned with the role complexity, rather than diversity, may have in generating or prohibiting stability. Food web models, for instance, are perhaps the most common type of model used to represent biological communities in ecology today. They usually represent interspecific species interactions by linear relationships between variables, which has two advantages.[148] First, assessing the complexity of these models is straightforward (see Ch. 2, §4; Ch. 5, §6). Second, a well-developed mathematical theory of Lyapunov stability and well-known techniques for evaluating it, such as the indirect method, ensure evaluation of the stability of these models is similarly straightforward (Hastings 1988; Paine 1988; Ch. 4, §2.4). A large body of work on food webs since May's (1974) influential monograph has subsequently exploited these facts to uncover properties of community structure that might produce Lyapunov stability.[149]

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[148] Graphically, links between nodes represent interspecific species interactions in a food web graph; the nodes represent the species comprising the community.

[149] See Paine 1980, Pimm 1982, Cohen *et al*. 1990, Pimm *et al*. 1991, and McCann 2005 for reviews.

These two advantages obviously encourage this modeling strategy, but at the cost of decreasing ecological realism.[150] The problem is that actual species interactions probably rarely take the linear form presupposed by these models, which means food webs typically poorly represent the dynamics of real-world biological communities.[151] Species interactions can be linearized in the infinitesimal neighborhood of an equilibrium (or any other point of state space), but Chapter 4, Section 2.5 explains why this severe restriction precludes reliable inference about how actual communities respond to perturbations, which are not of infinitesimal magnitude. It is unreasonable to suggest, for example, that a system like a biological community initially at equilibrium would remain in an *infinitesimal* neighborhood of it following typical real-world perturbations, such as frosts, droughts, increases in certain compounds (as caused by fertilizer runoff or a chemical spill for instance), *etc*. Thus, the fact that structural properties of food webs generate or jeopardize local Lyapunov stability indicates little about the relation between stability and complexity in actual biological communities, especially since ecological stability is poorly defined as local Lyapunov stability (see Ch. 4, §2). For precisely this reason, Hastings (1988, 1665) warned, "food web theory is not an adequate approach for understanding questions of stability in

[150] For a more detailed analysis of tradeoffs involved in scientific modeling see Levins (1966), Orzack and Sober (1993), Weisberg (2004), and Justus (2005).

[151] Some ecologists also criticize that most food webs are drastically incomplete and poorly constructed (see Paine 1988 for example). Thanks to Eric Pianka for bringing this criticism to my attention.

nature." It certainly tempers claims that recent advances in food web theory suggest a resolution of the SDC debate (*e.g*. McCann 2000; see Sarkar 2005a).

The evaluation of stability-complexity relationships for models that more accurately represent community dynamics presents different difficulties. One is the challenge of integrating different types of model properties into a general measure of ecological complexity for realistic, nonlinear models of biological communities as opposed to unrealistic models that represent species interactions with linear differential equations (see Ch. 5, §6). Another difficulty is evaluating the stability of these models. If, as is commonly assumed within mathematical ecology, Lyapunov stability adequately defines ecological stability, the ecological stability of nonlinear community models can be assessed with analytic techniques such as the direct method (Hirsh and Smale 1974; see Ch. 4, §§2.3–2.4). An unequivocal relationship between Lyapunov stability and model complexity (gauged informally), however, has not emerged. Realistic increases in model complexity sometimes decrease the likelihood of stability, but sometimes increase it. May (1974), for instance, found that including environmental stochasticity and realistic time delays in Lotka-Volterra models of predator-prey communities destabilized them, while incorporating spatial heterogeneity and more realistic predator responses to prey were stabilizing. The more realistic and complex the community model, moreover, the less mathematically tractable it and the assessment of its stability properties become. Since no general method for

evaluating the non-local Lyapunov stability for nonlinear systems is known (see Ch. 4, §2.5), the ultimate verdict on the relationship between Lyapunov stability and complexity remains unclear.[152]

The common assumption that ecological stability is adequately defined as Lyapunov stability, however, should be rejected. The reason, Chapter 4, Section 2 argues, is that Lyapunov stability only considers a community's response to perturbations that are accurately represented as temporary changes in species abundances (*i.e.* P_v perturbations), whereas ecological stability also concerns the community's response to perturbations that are only accurately represented by temporary changes in environmental parameters as well as species abundances (*i.e.* P_p and P_{vp} perturbations). As such, Lyapunov stability provides only a partial account of the kind of perturbation response ecological stability requires of a biological community. Unfortunately, a mathematical theory of stability for this more general class of perturbations has not yet been applied within ecology.

A recent study of realistic community models that does not presuppose that Lyapunov stability adequately defines ecological stability found that communities with many weak and few strong interspecific interactions exhibit fewer, and less severe oscillations, and therefore have a higher likelihood of

[152] Serious doubts about the robustness of May's (1974) finding of an inverse relationship between local Lyapunov stability and the complexity of linearized models of biological communities have also been raised. Besides the criticisms of DeAngelis (1975), Lawlor (1978), and Yodzis (1981) (see Chapter 2, §4), Haydon (1994, 2000) has also recently shown that if the linear differential equations May (1974) analyzed are made more biologically realistic, a positive relationship between stability and complexity emerges.

persistence (McCann *et al*. 1998). As a hypothesis about a putative positive stability-complexity relationship, however, results of this analysis are limited by: (i) the small size of the communities modeled (at most four species); and, (ii) the inadequacy of measuring ecological stability as persistence. As Chapter 4, Section 1.3 explained, however, persistence is clearly a plausible necessary condition for a community to be ecologically stable, but it is also much weaker than what ecological stability requires of biological communities.

Besides these difficulties, accurate empirical estimation of parameters of difference or differential equations used to model biological communities is often practically impossible given the significant monetary and temporal constraints on ecological research, especially for more complicated and realistic models. Community dynamics are even less likely, moreover, to be simply discernable from the limited data usually available.[153] For these reasons, more empirically oriented ecologists have focused instead on evaluating stability-diversity relationships with statistical measures of both concepts derived from data, rather than relying on difference or differential equations to model biological communities.

Like the theoretical approach, this strategy also faces difficulties, the most daunting of which is the lack of sufficient data. Their absence explains why

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[153] See Connell and Sousa 1983 for a review of methodological problems confronting this undertaking.

species richness, which is a poor measure of ecological diversity, has been used in almost all studies of stability-diversity relationships:[154] the data on species abundances required to assess the evenness of a community can rarely be collected, whereas the numbers of species often can be determined empirically. For instance, most of David Tilman's analyses of Minnesota grasslands (*e.g.* Tilman 1996, 1999; Lehman and Tilman 2000), which are probably the most spatially and temporally extensive empirical studies of stability-diversity relationships, measure diversity as species richness. His finding of a positive correlation between grassland species richness and the constancy of the total biomass of the grassland therefore shows little about the relationship between diversity and ecological stability because species richness is a flawed measure of ecological diversity. Pfisterer and Schmid (2002), for example, found that resistance and species richness were inversely related with respect to drought perturbations in a grassland in Switzerland.

Absence of adequate data also accounts for the prevalence of constancy as the measure of ecological stability in most empirical studies of the SDC debate, David Tilman's "temporal stability" being the most prominent example (see Ch. 4, §1.3). Lehman and Tilman (2000, 535) suggest that temporal stability is "readily observable in nature," as one reason for using it to measure ecological

[154] A recent study by Tilman *et al*. (2006) that uses the Shannon index to measure the diversity of a Minnesota grassland and finds the same positive correlation between species richness and temporal stability may be the only exception.

stability. It only requires, specifically, data on species biomasses. This contrasts with the fact that stability analyses of common community models only reliably indicate stability properties of real-world communities if models' parameters can be empirically estimated with sufficient accuracy. The problem, they suggest, is that sufficiently accurate parameter estimation is usually infeasible.

Enhancing measurability, however, does little to overcome the significant shortcomings of *defining* ecological stability as constancy, and the serious limitations of constancy measures like temporal stability as measures of ecological stability (see Ch. 4, §1.3). Specifically, their suitability depends upon:

(i) whether (and how diversely) the community is perturbed during the time period its constancy is assessed, which determines the measure's accuracy as an indicator of the community's response to perturbation; and,

(ii) whether the reference state is a point equilibrium, so that species biomasses will remain constant if unperturbed.

A community that resides in a relatively unvarying, unperturbing environment over the period it is assayed violates (i). In addition, data are usually collected over short time periods given the usually significant temporal and monetary constraints on ecological research, so (i) is rarely satisfied.

With respect to (ii), the predominant focus on equilibrium models in ecology in the 1960s and 1970s has also been supplanted with a recognition that nonequilibrium models with complex dynamics like limit cycles and strange attractor sets may best represent many types of ecological systems (Wiens 1984; Chesson and Case 1986; DeAngelis and Waterhouse 1987). Since communities

exhibiting such limit cycles or strange attractors violate (ii), there may be widespread violation of (ii) across biological communities.

The concept of temporal stability has also catalyzed controversy about whether it biases the stability-diversity debate in the positive. Doak *et al*. (1998) argued that temporal stability necessarily increases with species richness because statistical averaging of fluctuations in species abundances (measured as biomass) will necessarily decrease fluctuations in overall community abundance (thereby increasing temporal stability), as species richness increases.[155] One assumption of Doak *et al*.'s argument was that the variance of each species abundance σ^2 is proportional to the square of its mean abundance μ (*i.e.* $\sigma^2 = c\mu^z$, where $z = 2$ and c is a constant). In response, Tilman *et al*. (1998) pointed out that the value of z for a given biological community is an empirical question, and its value determines whether temporal stability increases with species richness in the absence of other factors or not. For example, May (1974) analyzed a logistic community model that included random environmental "noise" in which $z = 1$. If $z > 1$, temporal stability increases with species richness; it decreases with species richness if $z < 1$. Tilman (1999) also showed that temporal stability may increase as species richness increases due to an "overyielding effect": temporal stability

[155] Tilman (1999, 1458) called this the "portfolio effect" in analogy with the well-known economic principle that diversified portfolios are less volatile.

increases because total community abundance increases with the number of species it contains (see Ch. 4, §1.3).

Regardless of the ultimate validity of the portfolio or overyielding effect hypotheses as explanations of Tilman's grassland data, they have limited bearing on the general stability-diversity debate. Since temporal stability and species richness are inadequate measures of ecological stability and diversity, respectively (see Ch. 4, §1.3; Ch. 5, §5), causes of relationships between them provide little insight into possible relationships between stability properties such as resistance, resilience, and tolerance, and defensible measures of ecological diversity, which must take evenness of a biological community into account. For these reasons, Tilman's (1999) careful analysis of how species richness can increase temporal stability should probably not be considered as even, "a partial resolution of the long-standing diversity-stability debate" (Lehman and Tilman 2000, 548).

In conjunction with chapters 2, 4, and 5, the above discussion helps explain why the SDC debate remains unresolved. The concepts of ecological stability, diversity, and complexity are multifaceted and difficult to evaluate, theoretically or empirically. Consequently, only a few of the total possible stability-diversity and stability-complexity relationships have been analyzed thus far. These analyses, moreover, have focused on relations between tractable, but poor measures for the three concepts. Since ecologists disagree about how ecological stability and diversity should be defined, Chapters 4 and 5 propose and

defend adequacy conditions that help in the formulation of defensible definitions. The broad scope of the SDC debate and its potential implications for applied biological fields such as conservation, pest control, and resource management ensure its continued scientific scrutiny. The conceptual and methodological issues it raises merit more attention than thus far devoted to it by philosophers of science.

The SDC debate also broaches an issue fundamental to both science and philosophy, which is addressed in Chapter 3. At the core of the debate is the issue of how three specific ecological concepts should be defined. Abstracting from this specific issue, the debate raises the more basic question of how concepts should be defined in general. The views of scientists and philosophers generally diverge about the appropriate answer to this question, and reflect fundamentally different conceptions of the purpose of definition.

The main disagreement concerns the relationship between the meaning of the *definiendum* (the concept being defined) and its *definiens* (the concept(s) doing the defining), specifically, how similar their meanings should be. Typifying the views of most scientists but few philosophers, Rudolf Carnap's (1950) theory of explication answered this question in favor of requiring only a weak relationship between them (see Ch. 3, §2). Carnap (1950) presented explications of some simple empirical concepts such as 'fish' and 'temperature,' but the primary emphasis throughout his career was on the explication of theoretical

concepts such as analyticity, degree of confirmation, semantic information, *etc*. As a complex empirical concept, however, Chapter 3, Section 3 shows how proposed definitions of ecological stability also illustrate Carnap's most important adequacy criteria for explication: precision, fruitfulness, and similarity between the concept being explicated (the *explicandum*) and the concept(s) providing the explication (the *explicata*). It also suggests priority relations between them. Different definitions of the concept specifically show how these criteria can be satisfied in different ways.

Within philosophy, Carnap's account of explication attracted criticism, most notably from P. F. Strawson (1963), who objected that without strong similarity, perhaps even synonymy, between *explicandum* and *explicata*, explication is "utterly irrelevant" to the goal of philosophical clarification of concepts (see Chapter 3, §4). Carnap, on the other hand, was willing to sacrifice strong similarity to increase precision or fruitfulness with an explication. Their disagreement therefore turned on the relative import of different adequacy criteria for definition, specifically, similarity vs. precision and fruitfulness.

Chapter 3, Section 5 argues that this disagreement about how definitional adequacy should be assessed stems partly from different views of the purpose of definition and partly from disagreements about what best achieves those purposes. Definitions found in philosophy often attempt to maximize intuitive similarity with the imprecise concept being defined (DePaul and Ramsey 1998) – usually an

ordinary concept of natural language that philosophical scrutiny has shown to be problematic in some way – in an attempt to clarify and systematize relations between it and other natural language concepts. Analyses of intuitions about these concepts, though they often diverge significantly among philosophers, are therefore assumed to provide the main guidance about definitional content.

Definitions in scientific contexts, on the other hand, often sacrifice intuitive accord with the imprecise concept being defined to enhance formal rigor, experimental testability, measurability in the field, theoretical unification, integration with well-developed mathematical theories, *etc*. Proposed definitions of ecological stability provide a clear example of this. The objective is to improve against these benchmarks by establishing a relationship between concepts used in nonscientific contexts or in earlier stages of scientific development that fare poorly with respect to the benchmarks and concepts (ideally of well-confirmed scientific theories) that fare better against them. In other words, definitions should help facilitate in determining the structure of the world, which is not reliably achieved by inspecting intuitions.[156] Given this goal, Chapter 3, Section 5 argues definitions should be judged according to how they contribute to scientific practice – in helping generate predictions for instance – because science, rather

[156] The idea that some concepts better facilitate in determining the structure of the world than others should not be taken to presuppose some type of scientific realism. The facilitation in question could be evaluated in terms of empirical adequacy or the generation of new technologies, for instance, by instrumentalists.

than philosophical intuition, has best accomplished this goal. This was the principal motivation underlying Carnap's conception of explication.

Strawson (1963, 1992) and philosophers such as Moore (1942) and Sorenson (1991), however, regard definitions as the end products of conceptual analysis in which intuitions provide the primary guidance, and therefore *should* play the main role in constructing and evaluating definitions. This view of definition, or at least the idea that intuitions should play some nontrivial role in the formulation of definitions, is unproblematic if the definitional goal is simply to clarify the meanings of ordinary concepts of natural language. Besides intuitions, linguistic studies of how words are actually used by speakers of natural language (Jackson 1998), and studies of the mental representation of concepts in the cognitive sciences (Goldman and Pust 1998) also help achieve this goal. Results of such studies therefore could (and should) inform the defining process on this view. On the other hand, if the definitional objective is to improve our conceptual framework's ability to describe or determine what the world is like, this conception of definition is indefensible (see Ch. 5, §5).

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